THE
AMERICAN NATURALIST

VOL. XLVIII *February, 1914* NO. 566

SOME NEW VARIETIES OF RATS AND GUINEA-PIGS AND THEIR RELATION TO PROBLEMS OF COLOR INHERITANCE

PROFESSOR W. E. CASTLE

HARVARD UNIVERSITY

THE marvelous color variation of the domesticated animals has been recognized as a capital illustration of evolution from the time of Darwin to the present, and much study has been devoted to the question of how it has taken place. Nevertheless we have very little positive information as to how existing color varieties originated, and theories differ concerning the matter.

It becomes therefore important to record carefully any contemporary events which may throw light on the subject. This is my excuse for calling the attention of scientists to the recent appearance in England of two new and striking color variations of the common or Norway rat. I say "appearance" advisedly for it is impossible to say how long these variations may have been in existence within the race, cropping out perhaps from time to time sporadically. Certain it is, however, that they have only quite recently come to the attention of "fanciers," who have taken them up with great enthusiasm.

The new varieties are known to the fancy as (1) *pink-eyed* yellow, fawn, or cream; and (2) *black-eyed* yellow, fawn, or cream. From the evidence at hand it is clear that each of the two variations has originated *in the wild*

race and *as a mutation* or unit-character variation, *retrogressive* in nature (*i. e.*, due to loss of some normal constituent from the germplasm). Each is a simple Mendelian recessive character in crosses with wild race, and with certain at least of the tame varieties. The two variations have not as yet been combined by intercrossing, but this will be attempted soon and, I doubt not, with entire success.

My first information about the new variations was obtained from *Fur and Feather,* the official organ of the English fanciers, in which appeared advertisements of "the new variety" of black-eyed yellow rat. Now as long ago as 1903 Bateson had commented on the singular absence of a "yellow" variety among rats, noteworthy because nearly all mammals kept in captivity have such varieties; and I have since been bold enough to publish some speculations as to why this variation had not made its appearance. Consequently I was much excited to learn that it actually had appeared. Miss M. Douglas, one of the editors of *Fur and Feather,* and secretary of the National Mouse and Rat Club (of England) very kindly answered my inquiries about the new varieties and put me in communication with the "originators," who have given so clear and full accounts of their procedure in establishing the new varieties that even the genetic behavior of the variations is fairly certain, though I purpose to confirm this fully with experiments which are already in progress.

The pink-eyed variation made its appearance first, so far as known, about 1910 or 1911, but it had probably been in existence for some time and become rather widely diffused throughout the central part of England, for at about the same time pink-eyed wild rats were caught at or near Preston and at Chesterfield, cities some 65 miles apart. I am informed that Mr. T. Robinson at Preston and Mr. W. E. Marriott at Chesterfield independently established the "pink-eyed fawn" variety, or what would better be called the *pink-eyed agouti* variety, since appar-

ently it differs from the wild gray (or agouti) variety by the pink-eyed variation alone. It is not a true *yellow* variety at all genetically, though (like the pink-eyed gray mouse) it resembles one superficially because of the yellow ticking of the agouti fur.

It is also quite distinct genetically from the *albino* variation seen in white rats, yet its "dirty white" color is enough like the appearance of the albino to permit mistaking one for the other. Possibly this is why the pink-eyed variation may have been for some time overlooked.

Mr. Robinson has not answered my inquiries, but Mr. Mariott writes in detail about his observations and experiments.

Under date of October 11, 1913, he says:

The first rat with any semblance of fawn in it that I had was caught in a trap on a provision merchant's premises in Chesterfield. You could scarcely call it a fawn, but more of a cream or dirty white. I have also had four others similar to this one, 2 caught at the same place and 2 caught at a malt-house in close proximity to the other premises, [in all] 3 bucks and 2 does, but the only one that I was able to get to breed was the first brought to me, which was a buck. When first caught it was very wild, in fact it appeared to me to be more wild than an ordinary wild rat. It was a source of trouble getting it to mate, killing no less than 20 does before mating. I eventually got it mated to 2 does, one a pure white for at least 10 generations, and one black-and-white hooded-and-striped, or Japanese rat. The result of the pure white cross was 2 young, a buck and a doe, *which were agoutis with no white at all.*[1] The result from the Japanese cross was 7 young, 5 does and 2 bucks, which were the color of Irish agoutis being agouti color with a white stripe running underneath. These results naturally caused me great disappointment as I was expecting a fawn colored young one. When the young were old enough I mated father and daughter, result *nil;* mother and son, result *nil;* brother and sister. The brother and sister mating from the pure white cross produced 2 fawn colored rats, a buck and a doe, and 5 agoutis.[2] The brother and sister mating from the Japanese cross produced 2 fawn-and-white Japanese, 1 cream-and-white Japanese,

[1] Italics mine. Note the reversion to full wild color. This shows the pink-eyed variation to be entirely different in nature from the ordinary albino variation.

[2] Note the return of "fawn" (pink-eyed agouti) as a recessive character in approximately 1 in 4 young.

1 black-and-white Japanese, and 4 agoutis.[3] The fawns and fawn-and-whites resulting from these crosses were much deeper in color than the wild grandsire. Mated one with another they gave a proportion of about 2 fawn colored or fawn-and-white in 7 young.[4] I may say in conclusion that the original wild rat was in shape of body, skull, etc., as the ordinary brown or agouti rat that we have running wild in this district.

Mr. Marriott sold a "fawn-and-white" (pink-eyed hooded agouti) buck to Mr. E. F. Tilling, of Hessenford, who also "originated" the second variation, the "black-eyed yellow," or true yellow variation. His results from the pink-eyed variation confirm those of Mr. Marriott.

Mr. Tilling writes under date of October 18, 1913:

I see by *Fur and Feather* this week that you are interested in the yellow and cream varieties of rats. I am also much interested in these and have produced the latter variety within the last few months. We have 2 kinds over here, the yellow-and-white hooded with pink eyes and the self yellow (and cream) with black eyes. Both are quite distinct. The first mentioned was produced some 2 or 3 years ago. Mr. Marriott, of Chesterfield, bred the first I heard of from a wild caught fawn. He bred a couple of yellow and white hooded bucks of which Miss Douglas bought one and I the other. I mated mine to about 15 does of various colors and definite strains. He was a splendid breeder and got some very fine youngsters, but *not one of his own color from the first cross.*[5] I subsequently mated him to some of his daughters and they produced a good proportion of yellow-and-white young.[6] These are now fairly plentiful over here and are in the hands of several fanciers.

Of the other kinds, black-eyed fawns and creams, the first one exhibited and from which all mine are descended, was a very fine wild caught, deep colored, fawn specimen. I got her partly tame and exhibited her at the National Mouse and Rat Club's annual show at Bristol on November 27 and 28, 1912, where she won first in the self class and

[3] "Fawn- and white Japanese" means (to me) pink-eyed agouti with the "Japanese" color pattern (hooded). The formation of this class of young shows the hooded pattern ("Japanese") to be independent in transmission of the pink-eyed variation. "Cream-and-white Japanese," I interpret as pink-eyed *black* (non-agouti) hooded. "Black-and-white Japanese" is the familiar black hooded. We should expect this mating to produce also *self* pink-eyed agouti and *self* pink-eyed black which are not mentioned.

[4] The Mendelian expectation is 2 in 8.

[5] Italics mine. Note again the recessive nature of the variation.

[6] Not real yellow-and-white, as already explained, but pink-eyed agouti-and-white or black-and-white.

was well commented upon in the fanciers' papers. From this doe I have built up my strain of black-eyed creams. I mated her to a self black buck and she bred 8 youngsters all wild colored.[7] This is the only litter I had from her, as shortly afterward, during my illness, my man while transferring her from one cage to another let her get away and was unable to recapture her. However, I have bred from her youngsters, mating brother and sister, and the litters have invariably contained at least 1 fawn or cream[8] each time. I have now just bred for the first time from the 3 first does so produced, again mating them to their brother and the result is litters of 7, 5 and 7, respectively, all self creams.[9]

From the statements of Messrs. Marriott and Tilling, it is evident that the two variations, which they, respectively, have introduced into the rat fancy, are both recessive in heredity, as are also the three previously known Mendelizing color variations of rats, viz., (1) the albino variation (with uncolored coat and eyes); (2) the black variation (lacking the agouti ticking of the fur); and (3) the piebald "hooded" pattern of white and colored fur. Each of these is known to be an independent Mendelizing unit-character. If the new variations are as supposed independent of each other and of those previously known, they will make possible the immediate four-fold increase in number of the previously known color varieties of rats. If for the present we adopt a simplified terminology (as I have elsewhere suggested) for the different color variations, employing small letters for such as are recessive in heredity, we may use the following set of symbols:

White (albino) $= w$,
Black $= b$,
Hooded $= h$,
Pink-eyed $= p$,
Yellow $= y$.

[7] This shows that the original yellow animal was potentially an *agouti*. A pair of yellows which Mr. Tilling has sent me have *light bellies* and I presume are also potentially agoutis.

[8] "Cream" here probably means yellow not transmitting agouti. It probably lacks the lighter belly as do yellow rabbits which do not transmit agouti.

[9] This shows that extracted yellows breed true to yellow. Hence the variation is recessive, as in rabbits and guinea-pigs, not dominant as in mice.

By various combinations of these variations, if each is independent of all the others, 32 varieties become possible. Half of these varieties will be albinos, white and so visibly indistinguishable. The other 16, we have reason to suppose, will look different from each other. Previously we had but four of these, the first four in the following list of the theoretically possible 16.

1. *Normal or wild* ..... *agouti.*
2. *b* ..... *black,*
3. *h* ..... *hooded,*
4. *bh* ..... *black hooded,*
5. *p* ..... pink-eyed,
6. *pb* ..... pink-eyed black,
7. *ph* ..... pink-eyed hooded,
8. *pbh* ..... pink-eyed black hooded,
9. *y* ..... yellow,
10. *yb* ..... yellow black (*i. e.*, non agouti yellow),
11. *yh* ..... yellow hooded,
12. *yp* ..... yellow pink-eyed,
13. *ybh* ..... yellow black hooded,
14. *ypb* ..... yellow pink-eyed black,
15. *yph* ..... yellow pink-eyed hooded,
16. *ypbh* ..... yellow pink-eyed black hooded.

Varieties 1–4 have been known for some time; they have constituted the fancier's entire repertoire up to the present time. Varieties 5 and 9 have apparently arisen as wild sports obtained by Marriott and Tilling, respectively. By crosses these gentlemen have apparently obtained varieties 6, 7, 8, and probably 10. Varieties 11–16 are as yet unknown, but will doubtless soon be produced. Corresponding with each of the 16 colored varieties, an uncolored one should be possible of production, which would transmit in crosses with any colored variety the characteristics indicated by its formula. Albinos corresponding to colored varieties 1–4 are positively known to occur; their symbols would be *w*, *wb*, *wh* and *wbh*, respectively. Symbols for the remaining 12 expected varieties may be formed in like fashion, by prefixing *w* to the combinations already given.

All the five unit-character variations, which in different combinations are responsible for the color varieties of

rats, have their parallels in other mammals. Albinism and white-spotting (which in rats takes the form of the hooded pattern) are among the commonest. They occur in practically all mammals from mice to men. Albinism appears to consist in such a modification of metabolism that the process of pigment-formation can take place only feebly or not at all. That particular process which seems chiefly affected is the production of yellow pigment. Albinos, so far as I know, never produce genuine yellow pigment, though they may produce considerable quantities of black or brown pigment, as in the case of the Himalayan rabbit. An undescribed variety of guinea-pig, which I obtained about two years ago in Peru, may bear as much *black* pigment in its coat as wild cavies do, yet it forms no yellow pigment at all. Further this variation behaves as the allelomorph of ordinary albinism, indicating that it is probably of the same genetic character. For this reason *we may provisionally consider the albinism of mammals as due to a loss of the ability to form yellow pigment.* This usually, if not always, involves a lessened capacity to form other pigments also, so that it seems probable that the same chemical process, which produces yellow pigment as an end-product, is ordinarily involved also in producing the higher oxidation stages seen in brown and black pigment. In albinos this process would seem to be omitted, or to be accomplished by some step which does not involve the production of yellow pigment.

The yellow variation is extremely common in mammals. Yellow varieties, which at opposite extremes of intensity of pigmentation are known as *cream* and *red,* occur among horses, cattle, hogs, cats, dogs, rabbits, guinea-pigs, mice and human beings. In this variation pigment oxidation stops at the yellow stage, usually throughout the coat but not in the eye. Described in negative terms a yellow variety is one in which black and brown are suppressed or restricted. Black and brown, though usually restricted to the *eye* in yellow varieties, may occur also in

small quantities in the fur. Examples are found among horses (bay and dun varieties), cattle (the Jersey breed), dogs (the common dirty yellow variety), rabbits (the "tortoise-shell" variety), mice and guinea-pigs, and probably red-haired human beings also.

Black varieties of mammals arise in two genetically distinct ways. One is a quantitative increase or extension of black, the reverse of what happens in yellow varieties, so that black encroaches on regions normally yellow or may even obliterate them altogether. Examples are found in black squirrels, in which the agouti yellow ticking of the fur is almost, but not quite, obliterated by black pigment. But the "black" variation of rats, mice, guinea-pigs and ordinary rabbits results from a total loss, not a covering up, of the yellow ticking of the fur seen in agouti varieties. Genetically it is quite distinct from the other kind of black. It is a recessive variation and so breeds true.

The *pink-eyed* variation is the rarest of all the five enumerated as occuring in rats. It has been known heretofore only in mice, though I have recently obtained it also in guinea-pigs from Peru, where it seems to be well established.

In this variation the capacity to form yellow pigment is unimpaired, but only *traces* of black or brown pigment are produced. Consequently varieties which possess the other genetic factors of normal yellow animals have fully pigmented (yellow) fur, but with very faintly pigmented (pink) eyes, when they possess this factor. If, however, they possess the other genetic factors of black, brown, or agouti varieties, along with this pink-eyed variation, then both the fur and the eyes are very faintly pigmented. From this results the seeming paradox that pink-eyed blacks are less heavily pigmented than pink-eyed yellows, so that in rats the fanciers have called the former "creams," the latter "fawns."

When pink-eyed animals are crossed with albinos, offspring fully colored (eyes and all) result, as was first

shown by Darbishire some ten years ago. This indicates that the two variations are not only genetically distinct, but are physiologically complementary. The albino has defective metabolism for producing yellow (and in consequence brown and black also); the pink-eyed animal has the full mechanism for forming yellow, but its brown and black producing mechanism is defective. Together they possess the full mechanism of normal color production. Hence the reversion on crossing.

White spotting is clearly due to neither of the above modifications, but to a different change in the metabolism so that no pigment at all is produced. For an albino rabbit or guinea-pig may, as already observed, bear considerable black or brown pigment, but a white spot either on an albino, on a pink-eyed animal, or on a fully colored animal is entirely devoid of pigment. The paradox of a white spot on an albino is obtainable by crossing a white-spotted colored race with an albino race, which develops some pigment in the fur, as for example the Himalayan race of rabbits and guinea-pigs. In this way English-marked Himalayan rabbits and spotted albino guinea-pigs have been produced in my laboratory.

Postscript: While this paper was in press, Mr. Tilling, in reply to a further inquiry, wrote that his original black-eyed yellow rat was caught on a ship at Liverpool. The fact that the pink-eyed variety was found in the same general region leads him to believe that both variations were introduced on ships from some foreign country. It would be of much interest to know from what country or countries. Any information on this point obtainable from rat-catchers or others would be welcome.

"DOMINANT" AND "RECESSIVE" SPOTTING IN MICE

C. C. LITTLE,

BUSSEY INSTITUTION, HARVARD UNIVERSITY

INTRODUCTORY

THE inheritance of spotting has long proved of interest to animal geneticists. The nature of spotting is such as to afford an excellent chance to observe quantitative fluctuation and variations of very minute size. Furthermore, the fact that spotted varieties are found in all the rapidly breeding smaller domesticated mammals has led to a widespread investigation of its phenomena of inheritance.

One of the most clean-cut and constant types of spotting which has been studied is that of the "hooded" pattern in rats. This character was studied independently by Doncaster (1905) and by Castle and McCurdy (1907). All these observers agree that this form of spotting is due to a recessive Mendelizing unit which gives a 1:3 ratio in crosses with self-colored races.

In mice there has been no such well-localized pattern recorded and a series of spotted forms has been described which vary from black-eyed whites on one end of the series to heavily colored animals having only a few white hairs on the forehead or on the belly at the other extreme.

Cuénot, who did considerable work on the inheritance of spotting in mice, came to the conclusion that spotting is due to a group of recessive spotting factors which he describes as *p*1, *p*2, *p*3, *p*4, etc. His figures, however, show a single unit character difference as 3:1 and 1:1 ratios prove.

Up to 1908 all the spotting in mice was classed as recessive to solid-colored coat. At that time, however,

Miss Durham described the appearance of dominant spotting in addition to the recessive form which she also had experimented with. Such a dominant form of spotting is supposed, by Bateson, to be due to the addition of some factor for restriction of pigment formation in certain areas. This produces a dominant form of spotting as contrasted with the recessive type, which, he holds, is due merely to the loss of the "self" factor.

Hagedoorn (1912) gives data to show that the dominant form of spotting occurs in mice and in addition considers it as produced by a factor analogous to that which produces the dominant "English" spotting in rabbits.

The object of this paper is to present certain evidence concerning the nature of dominant and recessive spotting in mice; to discuss in its light the results of the above-mentioned investigations; and to criticize one additional point in Hagedoorn's work with mice.

Experimental

Materials.—Among several wild mice caught during the spring of 1911 was one individual with a white spot or "blaze" on the forehead between the eyes. This spot or "blaze" was about one quarter of an inch in length and one eighth of an inch in width. This mouse, an adult male, was transferred to a breeding cage and a series of experiments was started to determine whether the "blaze" character was inherited and, if so, in what way. As at that time no adult wild females were available from unrelated stock the wild "blaze" male (*S*1) was crossed with a female from a dilute brown race. In many ways this dilute brown race was the best possible material for such a cross. It was very closely inbred, being descended from a single pair of animals, progeny of which had been free from out-crossing for more than a year. Further, it had never given, nor has it ever given in hundreds of young, an animal with the slightest trace of a spot, even on the tail, where white bands are frequently seen in wild mice. Besides this the race was vigorous and active and yet easy to handle.

RESULTS

As a result of mating *S*1 "blaze" with a female of this dilute brown race, two litters, totalling eight young, were produced. All these young were self-colored without a trace of white, and, as expected, all resembled the male in coat color.

The F_1 generation selfs were then crossed in two ways, (1) *inter se* and (2) with animals of the dilute brown self race to which their mother belonged. It is hoped that a detailed account of all the matings made may be published later, but for the present purposes certain of the crosses under the first heading will suffice.

When F_1 was crossed *inter se,* two sorts of young were produced, namely, those with white and those without. While all of the latter type may be classed as self, the former were of two general sorts: (1) those with a "blaze" as large or larger than that of *S*1, these we may call "blaze" animals; and (2) those with only a *few white hairs* on the forehead, which we may call few white-haired (f.w.h.) animals.

The exact numbers in this cross were

Parents	Offspring		
	Self	F.W.H.	Blaze
*S*6 × *S*5—*S*8	11	3	3
*S*19 × *S*8	10	13	6
*S*18 × *S*8	3	1	2
	24	17	11

When the F_2 few white-haired animals were bred together they produced three types of young: *few white-haired, blaze* and *self,* as follows.

Parents	Offspring		
	Self	F.W.H.	Blaze
3,030 × 3,028	11	6	—
3,043 × 3,028	5	5	1
	16	11	1

One further fact is also of interest. Various descendants of F_2 "blaze" animals, which should breed as recessives,

have given the following results. The generation numbers may be disregarded as they refer to another method of classification. It is to be remembered that the parents in the tabulation given below, are all "blaze" in character.

Generation	Young Produced				
	Blaze	Blaze and Ventral White	F.W.H.	Self	Total
F_3B.....	33	6	4	1	44
F_4B.....	157	60	27	3	247
F_5B.....	70	53	5	0	128
F_6B.....	9	6	0	0	15
Total.....	269	125	36	4	434

If the "blaze" is a true Mendelian recessive we should expect all 434 offspring to have some white on them. The figures show that 430 of the 434 are of this type; that is to say, approximately 1 per cent. are self.

It is possible to account for the occasional production of selfs even if the "blaze" character is a true recessive, if we supposed that there are supplementary factors which may influence color development; and it is quite conceivable that such is the case.

The chief point of interest in the crosses given above is that while spotting behaves in F_1 *as a recessive, certain of the* F_2 *spotted individuals fulfil the requirements of dominant spotting by producing self offspring.*

The spotting came from a single individual and can scarcely be considered to be of two distinct types.

We may now consider the bearing of these results on the work of Miss Durham and Hagedoorn.

Miss Durham's Results

Miss Durham (1908) gives a detailed account of a recessive type of spotting in mice. The numbers she obtained are extensive, and the case seems well established, coming as it does in corroboration of the work of Cuénot, Darbishire and others. In the same papers she records the occurrence of a *dominant* spotted type of mice. Bateson (1909), commenting on the case, compares it with the

dominant "English" spotting in rabbits but also agrees that, in the case of mice, there is no criterion to enable one to distinguish somatically between the dominant and recessive forms. This, of course, is not the case in rabbits where the "English" pattern differs visibly from the "Dutch" spotting, which Hurst (1905) found to be recessive to self. Bateson also considers that the case of dominant spotting in mice, reported by Miss Durham, is the result of a different spotting factor from that producing recessive spotting.

In terms of the presence and absence hypothesis this means that the dominant form possesses a factor for restriction of pigmentation *which self forms lack.* This fact becomes of interest when Miss Durham's experimental results are closely examined.

In the race which gave rise to the dominant spotting the following conditions are seen.

A sooty yellow spotted mouse of unknown origin was crossed with a black-eyed white (spotted) animal (of Atlee's strain). Among other progeny was obtained a black-eyed white mouse with "agouti ears." This mouse, No. 21 (spotted), was crossed with an albino (carrying chocolate), No. 35, and gave among its progeny No. 69, *a black self mouse.* This black animal, No. 69 was crossed with an albino (carrying chocolate), No. 34, and from these two individuals came the dominant spotted race.

Now inasmuch as No. 34 and No. 35, the albinos, were not supposed to carry spotting, the dominant spotting must be considered as probably coming from No. 69, a *black self animal.* We know that *this animal must carry spotting as a recessive character* since its parent, No. 21, was spotted.

If, therefore, this animal was the progenitor of the dominant spotted race, and if he carried a recessive spotting, as it seems certain he did, we must suppose that one of three things has happened to the recessive spotting which he carried.

1. It may have been completely lost, failing to manifest itself in his germ cells.

2. It may have continued to exist and to be inherited together with the dominant type of spotting.

3. It may have been changed to a so-called "dominant" type of spotting simply by the nature of modifying supplementary factors which it encountered during ontogeny.

The first two cases necessitate the origin of the "dominant" spotting by a mutation in no way connected with the previous recessive spotting. In the first case, moreover, we should have to suppose the disappearance of the recessive spotting character in a manner entirely contrary to any principle of Mendelian heredity. In the second case the occurrence of the two types of spotting side by side in the same litters of young would so complicate the experiments that analysis would be difficult if not impossible, on Miss Durham's results.

There is good reason to believe that the third possible explanation is the correct one. It accounts for the formerly "recessive" type of spotting. It presupposes no fundamentally different appearance of the two types of spotting. Moreover, it is very probable that the albino race brings in the modifying factors necessary to give the apparent change in the type of spotting. The addition of a factor as presupposed by the presence and absence hypothesis is not proved by the results obtained nor is it necessary to account for them.

That the presence and absence hypothesis does not apply to all cases of spotting is seen in the case of the "blaze" mice in my experiments. Here, if F_1 animals had been given me as a starting point for experimentation, I should conclude the spotting to be recessive, while if F_2 spotted animals were given as a starting point the conclusion would be inevitable, that spotting should be considered dominant. Yet it is one and the same spotting in both cases. It is certain that "self" and "blaze" are alternative conditions, but it is equally certain that they differ from each other rather as two degrees of a

single process, one greater, the other less, than as the presence and absence of one or more unit characters.

HAGEDOORN'S WORK

Hagedoorn's work shows the danger of the modern tendency to produce factors upon the slightest provocation. While adding, in experimental work, only a single litter of young bearing on the problem, he gives a symbol for a factor for dominant spotting in mice, and further considers it as due to a factor similar to that producing the dominant "English" spotting of rabbits. He refers to Morgan's work with black-eyed white and self mice as being a study of this dominant factor in mice. Morgan himself suggests that if black-eyed white mice represent the extremes of the spotted series the appearance of spotted animals in crosses with selfs is due to a *strengthening* of the spotting factor or to a *change* in dominance. This is far different from supposing the addition of an entirely new inhibiting factor comparable to the English pattern in rabbits. Cuénot with mice and Castle (1905) with guinea-pigs have shown that black-eyed whites *are* the extreme of the recessive spotted series and it is almost certain that Morgan's explanation of the results, as due to *a change in dominance,* is the correct one. It is, of course, obvious that the presence and absence hypothesis fails to explain any change of dominance of a single character.

To treat "dominant" spotting in mice as due to the presence of a definite unit-character is exceeding present experimental facts, while to consider it similar in nature to the "English" spotting of rabbits is still less justified.

One other point in Hagedoorn's work is of such a nature as to require further experimentation before it can be accepted.

This is the case (on page 126) of "mutual repulsion between two factors." In this case, Hagedoorn mated together agouti animals heterozygous in factor *A* (for color production) and in factor *G* (for the agouti pattern).

Such animals would ordinarily form gametes *AG*, *Ag*, *aG* and *ag* in equal numbers. These by independent recombination would form

1 *AAGG*
2 *AaGG*
2 *AAGg*
4 *AaGg* } 9 agouti,

1 *AAgg*
2 *Aagg* } 3 black,

1 *aaGG*
2 *aaGg*
1 *aagg* } 4 albino.

But Hagedoorn gives figures which show that the proportion which he obtains is nearer 2 agouti; 1 black and 1 albino. This he supposes to be due to the fact that *A* and *G* can never go into the same gamete.

Now let us see what happens if this is the case. The original heterozygotes will form only two kinds of gametes instead of four, these will be *aG* and *Ag*. Now in the recombination of these gametes the following result will be obtained.

1 *aG aG* = 1 albino,
2 *aG Ag* = 2 agouti,
1 *Ag Ag* = 1 black.

So far, so good, but the trouble comes in testing the albinos. Here I may quote from Hagedoorn, p. 126:

> . . . thirteen of these albinos have been tested by mating with black. Without exception they have given black or equal numbers of black and albino young. . . . *But never has one of those albinos produced a single agouti young in a mating with black. Counting together the colored young of such families I get 89 black young.*[1]

This result is indeed remarkable, *for on Hagedoorn's own hypothesis* the albinos should have produced in such matings *nothing but agouti young,* "since they are all, by his hypothesis, homozygous for the agouti factor. The evidence is incontestable; *no repulsion of A and G can have occurred.* Has there been any coupling of these two factors? If such was the case only gametes *AG* and

ag would have been formed and this would have given only *agoutis and albinos* in a 3:1 ratio, while Hagedoorn reports "73 agouti, *37 blacks*[1] and 32 albinos."

The case then is nothing so simple as "repulsion" or "coupling," it includes *failure to segregate and complete disappearance of a dominant Mendelian factor; G the factor for agouti.*

Since numerous investigators of color inheritance in mice have never found the agouti factor anything but a normal Mendelizing factor epistatic to black, and since Hagedoorn himself seems to have become mixed in his interpretation, it seems that the case proves or shows little until a satisfactory answer can be found to the question of what has become of the agouti factor.

CONCLUSIONS

The facts above given lead to the following conclusions:

1. The so-called dominant type of spotting in mice does not differ from "self" color by the presence of a unit character which "self" lacks. The presence and absence hypothesis fails to account for the shifting dominance seen in spotting in mice.

2. It is misleading to describe, under the same symbol, the so-called "dominant" spotting of mice and the English spotting in rabbits.

3. It seems probable that differences in "dominance" of spotting in mice are due to modifying supplementary factors and such spotting might be termed "unsuppressed" and "suppressed" spotting rather than "dominant" and "recessive" in the Mendelian sense.

4. Hagedoorn's hypothesis of repulsion between the color factor, *A*, and the agouti factor, *G*, is incorrect.

November 19, 1913.

[1] Italics mine.

ON DIFFERENTIAL MORTALITY WITH RESPECT TO SEED WEIGHT OCCURRING IN FIELD CULTURES OF PISUM SATIVUM

DR. J. ARTHUR HARRIS

CARNEGIE INSTITUTION OF WASHINGTON

IN two papers which have already appeared in these pages,[1] I have shown that for the dwarf varieties of *Phaseolus vulgaris* the mortality of apparently perfect seeds (failure to germinate or to complete the life cycle) is not random, but differential, or selective.

It seemed highly desirable to extend these studies to other forms. *Pisum sativum* naturally occurred to me as affording suitable experimental material—both because of the wide range of seed characteristics and the convenience with which it may be bred. I had no pedigreed seed and consequently began work in the spring of 1913 with commercial stock. About 1,000 seeds from each of ten early (dwarf) varieties purchased from the Thorburn seed company were weighed, individually labelled and planted in short rows scattered over one of the fields of the Station for Experimental Evolution. Conditions were not the best, and the mortality was high.

Table I[2] gives the weights in units of .025 gram range[3]

[1] Harris, J. Arthur, "On Differential Mortality with Respect to Seed Weight Occurring in Field Cultures of *Phaseolus vulgaris*," AMER. NAT., 46: 512–525, 1912; "Supplementary Studies on the Differential Mortality with Respect to Seed Weight in the Germination of Garden Beans," AMER. NAT. [in press].

[2] For convenience the series may be designated by letters: *A*, Witham Wonder; *B*, American Wonder; *C*, Premium Gem; *D*, Little Gem; *E*, Nott's Excelsior; *F*, Sutton's Excelsior; *G*, Laxtonian; *H*, Little Marvel; *I*, Peter Pan; *J*, English Wonder.

[3] Class 1 = 0.000–.025 gram, . . . class 4 = .075–.100, class 5 = .100–.125, and so on. Thus to obtain means or standard deviations of weights in grams, deduct .5 from the values in the tables and multiply by .025.

TABLE I

WEIGHT OF SEEDS WHICH GERMINATED

Series	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Totals
A	1	6	31	64	65	100	75	57	42	19	6	1	1	—	—	—	—	468
B	—	—	—	—	40	107	134	170	105	35	12	1	—	—	—	—	—	604
C	—	—	3	5	53	117	173	126	56	11	3	2	—	—	—	—	—	549
D	—	—	—	3	36	106	191	167	80	18	4	1	—	—	—	—	—	606
E	—	—	—	5	49	105	105	68	32	3	—	—	—	—	—	—	—	367
F	—	—	—	—	9	27	63	96	86	69	26	11	4	—	—	—	—	391
G	—	—	—	—	1	7	27	71	114	159	132	81	23	16	—	—	—	631
H	—	—	—	1	17	44	116	183	151	63	20	6	2	—	—	—	—	603
I	—	2	—	2	6	8	16	25	51	88	127	126	101	55	17	8	1	633
J	—	—	—	17	107	126	142	112	41	13	5	2	—	—	—	—	—	565

TABLE II

WEIGHT OF SEEDS WHICH FAILED TO GERMINATE

Series	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Totals
A	4	16	49	63	102	90	93	78	42	16	2	1	—	—	—	—	—	556
B	—	—	—	2	—	52	104	117	84	36	3	—	2	—	—	—	—	400
C	—	2	1	12	56	116	122	95	34	18	4	1	—	—	—	—	—	461
D	—	—	1	5	37	88	127	93	37	11	—	—	—	—	—	—	—	399
E	—	—	—	13	115	210	180	91	23	4	1	—	—	—	—	—	—	637
F	—	—	—	—	13	46	84	125	153	114	49	16	10	3	—	—	—	613
G	—	—	—	—	5	6	29	43	75	85	70	42	13	7	—	—	1	376
H	—	—	—	1	17	66	71	110	93	29	14	3	—	—	—	—	—	404
I	—	—	3	1	13	18	26	35	29	60	65	62	31	22	3	2	4	374
J	—	—	—	13	55	88	125	91	53	12	2	—	—	—	—	—	—	439

of the seeds which germinated.[4] Table II gives the same distributions for the seeds which failed to germinate. The physical constants[5] with their probable errors are given in Tables III–IV.

Taking the differences, germinated *less* failed, in order to have the positive sign if elimination tends to increase mean weight or variability of weight and the negative sign if it tends to decrease these constants in the population of seeds which grow as compared with those which fail, I find the differences shown in Table V.

[4] When the plantlets were about three inches high the labels for seeds which had failed to germinate were collected. The distributions for the seeds which had germinated were then obtained by subtraction from the weight seriations prepared before planting. Some of the plants subsequently died.

[5] Sheppard's correction was applied to the second moments.

TABLE III

PHYSICAL CONSTANTS FOR SEEDS WHICH GERMINATED

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
A	9.254 ± .062	2.000 ± .044	21.610 ± .498
B	10.581 ± .038	1.371 ± .027	12.954 ± .256
C	10.078 ± .037	1.294 ± .026	12.844 ± .266
D	10.355 ± .033	1.211 ± .023	11.692 ± .230
E	9.790 ± .042	1.193 ± .030	12.185 ± .308
F	11.568 ± .054	1.571 ± .038	13.583 ± .334
G	13.090 ± .043	1.612 ± .031	12.313 ± .237
H	11.186 ± .037	1.362 ± .026	12.178 ± .240
I	14.269 ± .057	2.134 ± .041	14.958 ± .290
J	9.773 ± .040	1.429 ± .029	14.622 ± .300

TABLE IV

PHYSICAL CONSTANTS FOR SEEDS WHICH FAILED TO GERMINATE

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
A	8.993 ± .057	2.003 ± .041	22.286 ± .472
B	10.898 ± .041	1.236 ± .030	11.346 ± .274
C	9.913 ± .045	1.439 ± .032	14.512 ± .329
D	10.048 ± .041	1.229 ± .029	12.234 ± .296
E	9.488 ± .030	1.122 ± .021	11.826 ± .227
F	11.726 ± .045	1.653 ± .032	14.097 ± .277
G	12.816 ± .062	1.787 ± .044	13.945 ± .350
H	10.869 ± .049	1.447 ± .034	13.317 ± .322
I	13.225 ± .089	2.552 ± .063	19.298 ± .493
J	10.009 ± .044	1.376 ± .031	13.749 ± .311

TABLE V

COMPARISON OF PHYSICAL CONSTANTS FOR SEEDS GERMINATING WITH THOSE FOR SEEDS FAILING TO GERMINATE

Series	Difference in Mean and Probable Error of Difference	Difference in Standard Deviation and Probable Error of Difference	Difference in Coefficient of Variation and Probable Error of Difference
A	+ .261 ± .085	−.003 ± .060	−1.676 ± .686
B	− .316 ± .057	+.134 ± .040	+1.608 ± .375
C	+ .165 ± .058	−.144 ± .041	−1.669 ± .423
D	+ .307 ± .053	−.019 ± .037	− .542 ± .375
E	+ .302 ± .051	+.071 ± .036	+ .358 ± .382
F	− .158 ± .070	−.082 ± .049	− .513 ± .434
G	+ .274 ± .075	−.175 ± .054	−1.632 ± .422
H	+ .317 ± .062	−.085 ± .044	−1.139 ± .401
I	+1.044 ± .105	−.418 ± .074	−4.340 ± .572
J	− .236 ± .060	+.053 ± .042	+ .873 ± .432

Consider first the differences in the mean weight. Seven are positive and three are negative. All of the

seven positive differences are at least 2.5 times their probable error; four of them are over five times their probable error. The mortality is therefore almost certainly selective, with a tendency to leave the surviving population with seeds distinctly heavier on the average than those which were planted. On the other hand, there are the three cases in which the seeds which produced plantlets were on the average lighter than those which failed to germinate. One of these differences is only 2.2 times its probable error, and so perhaps not statistically trustworthy. Of the other two, one is over 5.5 times and the other nearly 4 times its probable error. There can be little doubt that in at least one of these cases there is a tendency for the lighter seeds to show a viability greater than that of the heavier. In garden beans, too, strong evidences of differences between strains in this regard have been pointed out.

The interpretation of the variabilities offers greater difficulties than does that of the means. More data and more refined methods of analysis are necessary for a final solution of the problem. It appears, however, that in seven of the ten series the variability of the seeds which survived is less than that of those which failed. This is true whether absolute variability as measured by the standard deviation or relative variability as expressed by the coefficient of variation be used in the comparison.

As far as these data go, therefore, they are in general accord with those for *Phaseolus*. In both of these Leguminosæ the mortality which occurs before germination is not random but differential. But in both cases, and especially in *Pisum* where the seeds used are of commercial, not pedigreed, stock and number as yet only about 10,000, far wider series of experiments and much refinement of methods of analysis are necessary to establish fully the nature and the immediate (physical or chemical) cause of this selective death rate.

COLD SPRING HARBOR, N, Y.,
July 28, 1913

THE INHERITANCE OF A RECURRING SOMATIC VARIATION IN VARIEGATED EARS OF MAIZE[1]

PROFESSOR R. A. EMERSON

UNIVERSITY OF NEBRASKA

INTRODUCTION

THE inheritance of variegation has special interest and importance in genetics. It is with forms of variegation that the only two certainly known cases of non-Mendelian inheritance have had to do. I refer to Baur's experiments with *Pelargonium,* in which crosses of green-leaved and white-leaved forms exhibited somatic segregations in F_1 that bred true in later generations, and to Correns's work with *Mirabilis,* which showed green and white leaf color, to be inherited through the mother only. De Vries's conception of "ever-sporting" varieties was apparently founded largely upon the behavior of variegated flowers in pedigree cultures, from which he reached the conclusion that the variegated color pattern and the monochromatic condition arising from it as sports are non-Mendelian in inheritance. Correns, however, has shown that in *Mirabilis jalapa* the inheritance of these sports is distinctly Mendelian, and the results of East and Hayes indicate the same for *Zea mays.* In this paper I shall present data from maize and attempt to show how they can be interpreted in strictly Mendelian terms.

Variegation is distinguished from other color patterns by its incorrigible irregularity. It is perhaps most often seen in the coloration of flowers and leaves but also occurs in fruits, seeds, stems, and even roots of various plants. It is characteristic of the ears of certain varieties of maize known, at least in the Middle West, as "calico" corn. In

[1] The experimental results reported here were presented at the Cleveland meeting of the American Society of Naturalists, January, 1913. Research bulletin No. 4 of the Nebraska Agricultural Experiment Station.

these varieties the pericarp of most of the grains has few to many narrow stripes of dark red, the remaining area being colorless or showing a sort of washed-out red. Often broad red stripes appear on some grains, a single stripe covering from perhaps one tenth to nine tenths of the grain. Not uncommonly there are entirely colorless grains (so far as pericarp is concerned) and also solid red grains scattered over the ear. Much more rarely there is found a "freak" ear with a large patch of self-red or nearly self-red grains. Or sometimes an ear is composed largely of red or almost red grains with a small patch of striped or nearly colorless grains. In such cases it is not uncommon for the margin of the red area to cut across a grain so that one side—always the side toward the red patch—is red and the other side colorless or striped. Ears that are colorless throughout, except for a single striped grain, are not unknown and there are even known ears that are red except for a single striped grain. Very rarely a plant has one self-red ear and one variegated ear on the same stalk. It is also conceivable that all the ears of a plant might thus become red, but of course such a red-eared plant rising as a bud-sport could not ordinarily be distinguished from a red-eared plant arising as a seed-sport.

Variegated ears generally have variegated cobs, the amount of red in the cob ordinarily varying with the amount of red on the grains. In some "freaks" a part of the cob is solid red and the rest variegated. In a few such cases the red part of the cob corresponds exactly in position to the freak patch of grains. This is more frequently true when the grains of the freak patch are dark variegated than when they are self-red. In other ears there is no change in the cob corresponding to the change in the grains. The husks of variegated ears are also rather commonly variegated. In a few freak ears the red side of the ear is enclosed in reddish husks, the remainder of the husks being light striped. Red-eared plants arising as seed-sports always have solid red cobs and usually solid reddish husks.

The first account, so far as I am aware, of the inheritance of the striking somatic variations so commonly found in variegated plants was given by de Vries[2] in his discussion of ever-sporting varieties. The study was made in the years from 1892 to 1896 with a variety of *Antirrhinum* with striped flowers. De Vries's records are reproduced diagrammatically in Fig. 1.

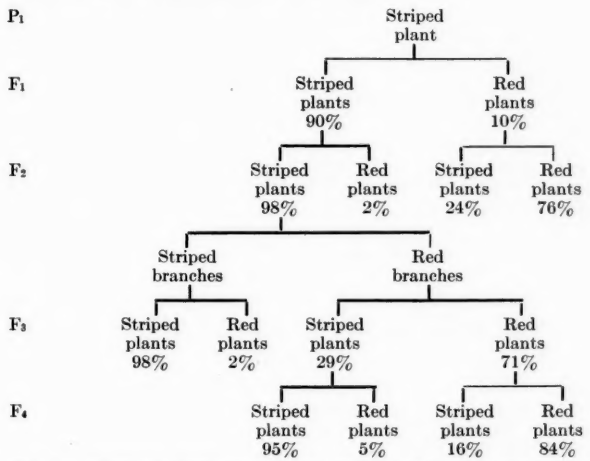


FIG. 1. DIAGRAM FROM DE VRIES'S RECORDS SHOWING THE INHERITANCE OF VARIEGATION AND SELF-RED IN THE FLOWERS OF *Antirrhinum*.

Of these results de Vries says:

From these figures it is manifest that the red and striped types differ from one another not only in their visible attributes, but also in the degree of their heredity. The striped individuals repeat their peculiarity in 90–98 per cent. of their progeny, 2–10 per cent. sporting into the uniform red color. On the other hand, the red individuals are constant in 71–84 per cent. of their offspring, while 16–29 per cent. go over to the striped type. Or in one word: both types are inherited to a high degree, but the striped type is more strictly inherited than the red one.

De Vries's results were in some respects very similar to those of Correns and it is probable that he would have interpreted them in the same way had he then been familiar with Mendelian phenomena.

[2] Vries, Hugo de, "Species and Varieties," pp. 309–328 (1905).

Correns[3] has reported results of a careful study of the inheritance of the self-green condition appearing as a bud-sport on variegated-leaved plants of *Mirabilis jalapa,* and also of a self-color appearing in striped-flowered plants of the same species. His results for self-green and variegation of the leaves are shown diagrammatically in Fig. 2. The results are stated in approximate percentages. I have seen no report in which the detailed records were given.

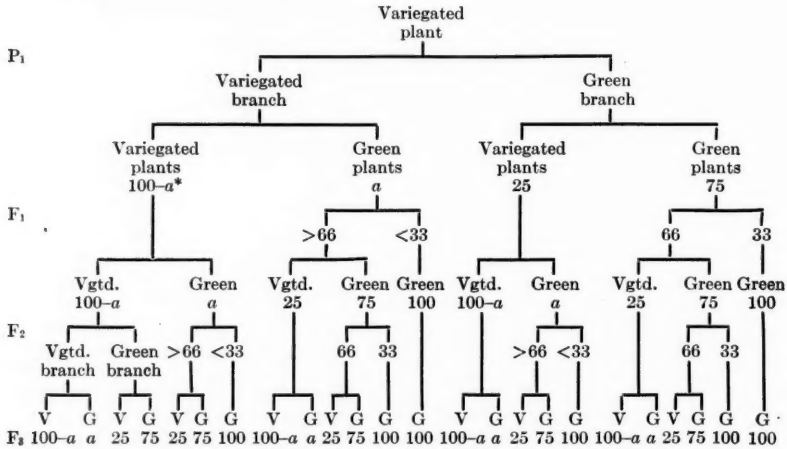


FIG. 2. CORRENS'S DIAGRAM SHOWING THE INHERITANCE OF VARIEGATION AND SELF-GREEN IN THE LEAVES OF *Mirabilis jalapa.*

The diagram shows that a variegated branch of a variegated plant produces in F_1 mainly variegated plants, but occasionally a wholly green plant, while a green branch from the same plant produces in F_1 25 per cent. variegated and 75 per cent. green plants. The F_1 variegated plants, however produced, behave in later generations just like the original variegated parent plant. The F_1 green plants, whether produced from green or variegated branches, are always of two sorts, namely, those that are homozygous and therefore breed true green, and those

[3] Correns, C., *Ber. Deutsch. Bot. Gesel.,* 28: 418–434, 1910. *Der Uebergang aus dem homozygotischen in einen heterozygotischen Zustand im selben Individuum bei buntblättrigen und gestreiftblühenden Mirabilis-Sippen.*

* Numerals indicate approximate percentages; $a = 0$–10 per cent.

that are heterozygous and therefore produce progenies of green and variegated individuals in a ratio of approximately 3 to 1. Correns points out that a green branch of a variegated plant behaves as though it belonged not to a variegated plant at all, but to a hybrid between a variegated plant and a green one, in which green is dominant, and that half of the germ cells produced by the green branch carry a factor for green and the other half a factor for variegation. Similar results were secured from branches with self-colored flowers on plants with striped flowers, except that such branches produce few if any more self-colored plants than are produced by branches with striped flowers. Plants with self-colored flowers, no matter how they arise, behave as they would if they had occurred in an F_2 progeny of a cross of striped by self-colored plants.

Results of Experiments with Maize

Hartley[4] in 1902 gave an account of an experiment with variegated maize. In a comparatively pure white strain, which occasionally produced a red ear, there was found an ear similar to some of the "freak" ears noted earlier in this paper. It is described as being red except for a spot covering about one fifth of the surface, in which the grains were white with fine red streaks. The excellent plate accompanying the account, however, shows that most of the "red" grains had white streaks at the crown and that the cob was light-colored, not red. From the near-red grains of this ear there was produced a crop of 84 red ears and 86 pure white ones, while from the variegated grains of the same ear there came 39 light variegated ears and 36 white ones. Hartley refers to the parent ear as a "sport or sudden variation from the type" but does not indicate whether the "type" in mind was the white variety or the red ears occasionally produced by it. Both the color of the grains and cob and the production of about 50 per cent. of white ears from both the red and the variegated grains indicate very clearly that the parent ear was a

[4] Hartley, C. P., Yearbook, U. S. Dept. Agr., 1902: 543–544.

heterozygous, variegated one and that it probably came from a white seed crossed by a stray grain of pollen from a variegated-eared plant, just as the occasional red ears in the white variety were certainly produced by stray pollen from red-eared plants.

More recently East and Hayes[5] reported like behavior of a similarly variegated ear. An ear having on one side solid red grains and on the other white and very light variegated grains, similar to some of the "freak" ears noted earlier in this paper furnished the material for the test. The ear was produced from a white seed in a field of otherwise pure white corn and was therefore doubtless heterozygous for pericarp color and was probably pollinated in large part from plants without pericarp color, so that 50 per cent. white-eared plants were to be expected in its progeny. The white, the light variegated and the solid red grains were planted separately. The white and the variegated seeds alike produced light variegated and white ears, 15 of the former and 15 of the latter. The red seeds produced 22 white ears and 22 solid red ears. The authors' interpretation of these results is that the white seed which gave rise to the original colored ear had been fertilized by pollen from a red-eared plant and that the F_1 plant, "due to produce a red ear, varied, somatically, so that one half of the ear was red and one half striped." The authors further state:

> This variation was transmitted by seeds, but at the same time the hybrid character of its seeds was unchanged as shown by their segregation into reds and whites in the next generation and the normal segregation of the hybrid dark reds in a further generation.

In the light of my own observations, it is equally possible and seems more likely that the white seed from which the original red-and-variegated ear came was the result of pollination from a plant with variegated ears, and that the somatic variation was from variegated grains to solid red grains rather than from red to variegated. But the important fact is that a somatic variation was later inherited in a strictly Mendelian way.

[5] East, E. M., and Hayes, H. K., Bul. Conn. Agr. Expt. Sta., 167: 106–107. 1911.

In 1909 I obtained results somewhat similar to those reported by East and Hayes. A few "freak" ears were secured, mainly from local and national corn expositions. Nothing was learned as to their parentage or pollination. Obviously, however, the parentage of the red, the variegated, and the white grains of any one ear was the same, and it is reasonable to suppose that the different sorts of grains of any one ear were pollinated with approximately the same kind or the same mixture of pollen. The results, as shown below, were essentially like those of Hartley and of East and Hayes.

Seeds Planted	Number of Plants with		
	Red Ears	Variegated Ears	White Ears
Self-red	43	0	33
Variegated and white	0	22	29

The results from four other ears were somewhat different, probably owing to differences in their pollination. (See Fig. 3.) They were as follows:

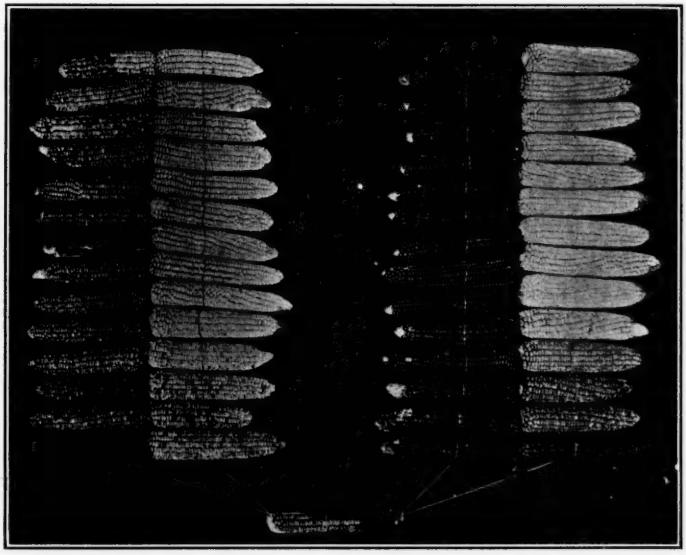


FIG. 3. *A*, "freak" ear of maize; *B*, progeny of striped seeds; *C*, progeny of self-red seeds.

Seeds Planted	Number of Plants with		
	Red Ears	Variegated Ears	White Ears
Self-red	128	32	69
Variegated and white	8	103	68

Two other ears of similar history, while they gave quite as striking results as those noted above, probably do not belong here since none of their immediate progeny were variegated and no variegated ears have occurred in later generations. These two ears were made up of red grains and white grains only. The results were as follows:

Seeds Planted	Number of Plants	
	Red Ears	White Ears
Red	77	85
White	0	122

The white ears bred true in later generations and the red ears produced reds and whites in typical Mendelian fashion. No such somatic variations as these have occurred in my cultures of self-red or white maize, so that I have been unable to study them further. Somatic variations in variegated corn, however, are not rare. Unfortunately several of the most pronounced of those occurring in my cultures were open-pollinated and therefore of little or no use in a careful study. I have therefore been obliged to make use in large part of the few solid red and nearly solid red grains scattered over otherwise more or less evenly variegated ears.

From twenty-three self-pollinated, variegated ears of plants that were homozygous for pericarp color, grains with various amounts of red were selected and planted. The results are summarized as follows:

Seeds Planted	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red Ears
Self-red	8	9	0
Nearly self-red	56	16	0
More than half red	9	34	0
Less than half red	5	22	0
Narrow red stripes	33	394	0
Non-red	1	22	0

Besides these 23 ears, 20 other selfed ears from homozygous plants contained only narrow-striped seeds from which there were produced 16 plants with red ears, 280 with variegated ears, and none with white ears. Similarly 21 selfed ears with narrow-striped seeds only, from plants that were heterozygous for pericarp color, produced 28 plants with red ears, 411 with variegated ears, and 208 with non-red[6] ears. Variously colored grains from 42 self-pollinated, heterozygous, variegated ears gave the following results:

Seeds Planted	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red[7] Ears
Self-red	15	1	6
Nearly self-red	17	8	8
More than one half red	46	51	31
Less than one half red	8	34	21
Narrow red stripes	57	767	300
Non-red	0	10	6

In the progenies of these 63 self-pollinated ears that were heterozygous for pericarp color, there were approximately 2.5 plants with pericarp color to one without it. All the classes of grains from self-red to non-red yielded both colored and non-colored ears, thus indicating, as already shown by East and Hayes, that the somatic variation in the seeds does not change their hybrid character. Considering only the plants with pericarp color, in the progenies of both heterozygous and homozygous variegated ears, 106 progenies in all, marked differences are seen in the percentages of self-red ears from seeds of the different color classes, as follows:

[6] Some of these ears had what I have termed "half-red" pericarp, *i. e.*, pericarp with a reddish color extending part way from the base to the crown of the seeds. (See Ann. Rpt. Nebr. Agr. Expt. Sta., 24: 62. 1911.) Half-red differs from self-red and variegated red not only in distribution but also in almost never developing fully in the heterozygous condition. It is hypostatic to self-red, but shows between the red stripes of variegated seeds. Since its presence does not mask either self-red or variegated-red and since it is strictly allelomorphic to both of them, half-red is here included with non-red. Variegated ears have never, in my observation, produced half-red grains as somatic variations.

[7] Some of these were half-red. See footnote 6.)

Seeds Planted	Number of Plants with		Per Cent. Self-red Among Colored Ears
	Self-red Ears	Variegated Ears	
Self-red	23	10	69.7
Nearly self-red	73	24	75.3
More than one half red	55	85	39.3
Less than one half red	13	56	18.8
Narrow red stripes	134	1,852	6.7
Non-red	1	32	3.0

In comparison with the cases reported by Hartley and by East and Hayes and one of my first cultures from open-pollinated ears, in all of which red grains produced no variegated ears and striped grains no red ones, the striking features of the results from these 106 self-pollinated ears are the facts that the wholly red grains yielded some variegated as well as red ears and that the striped grains and even the wholly non-red grains yielded some red as well as variegated ears. The percentages noted above indicate in a general way that for self-pollinated, variegated ears, *the more red there is in the seed planted the larger the percentage of red ears in the progeny.* These records, however, do not give a wholly trustworthy indication of the mode of inheritance of the somatic variations concerned here. If there is a modification of some factor in the female gametes, associated with a visible modification of somatic cells of the pericarp and even at times of the cob and husks, modifications that do not become visible until long after the gametes are formed, may there not be a similar modification of the same factor in the male gametes, though here not associated with any visible change in somatic cells because of the fact that the staminate inflorescence dies too soon after the pollen is shed? If male gametes do carry such modified factors and if the modification is as irregular in occurrence as the somatic modifications seen in variegated ears, so that any part of the tassel, from all to none, may produce gametes with the modified factor while not showing any visible somatic modification, it is obvious that the real nature of the male gametes of any variegated-eared maize plant can not be foretold. The mere fact that a variegated ear is self-pollinated, therefore, does not insure that its seeds are fertilized with pollen of known character.

That the male gametes of variegated-eared maize do often carry factors for self-red is shown by crosses of pure non-red strains with pollen from plants with variegated ears. The plants that furnished the pollen for these crosses were in some cases the same ones whose self-pollinated ears were concerned in the records discussed above. The results of these crosses are summarized here. Eight non-red ears crossed by plants that were homozygous for pericarp color yielded 17 red-eared, 116 variegated-eared and 8 white-eared[8] plants. Similarly, 14 ears of pure non-red strains crossed by pollen from plants heterozygous for pericarp color yielded 26 red-eared, 192 variegated-eared and 229 white-eared plants. Considering merely the plants with colored ears, 22 crossed ears produced 43 red-eared to 308 variegated-eared plants, or a little over 12 per cent. self-red.

Since the male gametes of variegated-eared corn have now been shown occasionally to carry a factor for self-red, it is obvious that only from crosses of variegated-eared plants with pollen from pure non-colored strains, can a definite idea of the inheritance of the somatic variations in pericarp color be gained.[9] Twelve ears from homozygous, variegated plants cross-pollinated by non-red strains might have afforded important evidence, but for the fact that 7 of them contained only narrow-striped grains and the other 5 no fully or even nearly self-red grains. The results are summarized here:

Seeds Planted	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red Ears.
More than one half red.....	5	11	0
Less than one half red.....	0	15	0
Narrow red stripes.....	2	281	0
Non-red.....	0	22	0

[8] Some of the 8 white ears may have been extreme light types of variegation, for in some other cases very light variegated and wholly white ears have been observed on the same plant. And of course some of them may have been due to accidental pollination of the parent ear.

[9] Though the genetic factors for pigment patterns in maize seem to be distinct from the factors for the pigment concerned in these patterns, no non-colored maize that I have used has ever given any indication in crosses of carrying pattern factors.

The principal facts of interest here are the production of only one red-eared plant to about 140 variegated-eared ones from narrow-striped seeds, and of about one red-eared to two variegated-eared plants from seeds with from one half to perhaps three fourths red.

Of 20 variegated ears, heterozygous for pericarp color, that were crossed with pollen from pure non-colored strains, 5 had only narrow-striped grains and 15 had variously broad-striped grains and even some self-red ones. The summaries of these crosses are as follows:

Seeds Planted	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red Ears
Self-red	9	0	11
Nearly self-red	5	0	2
More than one half red	4	2	2
Less than one half red	3	5	9
Narrow red stripes	7	265	301
Non-red	0	27	20

Here again, just as with homozygous, variegated ears, *the more red there is in the pericarp the more likely are the female gametes to carry a factor for self-red.* While the number of individuals dealt with are too few to afford reliable evidence, it is suggestive to note that the ratio of red-eared to variegated-eared plants, though not the ratio of red-eared to total plants, is greater in case of parent ears that are heterozygous than of those that are homozygous for variegated pericarp.

So far nothing has been said of the results in generations later than the one grown from the selected seeds (F_1). Let us now see what results follow when the variegated ears and the red ears produced as explained above become the parents of second generations (F_2) from the selected seeds. The variegated ears so produced behave like the original variegated ears from which seeds were selected and their progenies have, therefore, been included in the data already presented. There remains only to present the records of the progenies of red ears.

Data are available from 7 F_1 red ears obtained from self-pollinated, homozygous, variegated plants. Five of

these red ears were self-pollinated and two were crossed with pure white-eared plants. The results in F_2 and F_3 were as follows:

Seeds Planted from	Number of Plants with		
	Self-red Ears	Variegated Ears	Non-red Ears
F_1 reds from selfed, homo., vgtd. P_1's			
5 ears selfed	119	37	0
2 ears × white	46	45	0
F_2 reds from selfed F_1 reds			
1 ear selfed	9	2	0
1 ear selfed	16	0	0
F_2 reds from F_1 reds × white			
1 ear selfed	26	0	5
2 ears × white	40	0	37

The above is approximately what would have been expected, had *the F_1 red ears that arose from self-pollinated, homozygous, variegated-eared plants been produced by a cross between red-eared and variegated-eared races.*

Of the F_1 reds arising from self-pollinated, heterozygous, variegated-eared plants, nine were selfed and two were crossed with whites. The results secured in F_2 and F_3 follow:

Seeds Planted from	Self-red Ears	Variegated Ears	Non-red Ears
F_1 reds from selfed, hetero., vgtd. P_1's			
3 ears selfed (a)	104	23	0
1 ear × white	6	7	0
6 ears selfed	105	0	38
1 ear × white	12	0	7
F_2 reds from selfed F_1 reds of (a)			
4 ears selfed	59	12	0
1 ear selfed	23	0	0

From the above it appears that *the F_1 red ears, arising from self-pollinated, heterozygous, variegated-eared plants behave in some cases as if they were hybrids between red-eared and variegated-eared races and in other cases as if they were hybrids between red-eared and white-eared races.*

Of the four possible sorts of red-eared "sports" from variegated-eared plants, two remain to be treated. Be-

352 83

cause of their similar behavior they will be considered together here. Of the F_1 red ears arising from homozygous, variegated-eared plants that had been crossed with white-eared races, three were self-pollinated and two crossed with whites. Of the F_1 red ears arising from heterozygous, variegated-eared plants that had been crossed with white-eared races, four were selfed. The results in F_2 and F_3 are:

Seeds Planted from	Self-red Ears	Variegated Ears	Non-red Ears
F_1 reds from vgtd. P_1's × white			
P_1's homozygous			
3 ears selfed	54	0	16
2 ears × whites	34	0	43
P_1's heterozygous			
4 ears selfed	102	0	47
F_2 reds from selfed F_1 reds			
3 ears selfed	32	0	10
1 ear selfed	43	0	0

So far as these results go they indicate that *F_1 reds arising from crosses between both homozygous and heterozygous, variegated-eared plants and white-eared races behave as if they were hybrids between red-eared and white-eared races.*

One homozygous, variegated-eared plant was cross-pollinated by a homozygous red race. From the variegated ear produced, self-red, nearly self-red, and narrow-striped seeds were planted. All resulted, of course, in red-eared F_1 plants, 16 in all. A self-pollinated F_1 red ear from a narrow-striped seed gave in F_2 24 red-eared and 11 variegated-eared plants—somewhat fewer reds than were to have been expected. An F_1 red ear from a nearly self-red grain, when cross-pollinated with non-red, yielded 9 reds and 11 variegated in F_2. A third F_1 red-eared plant, this one from a self-red grain of the variegated parent ear, bred true red in F_2. One ear of this F_1 plant was selfed and yielded 14 reds in F_2, and another ear was cross-pollinated by non-red and yielded 29 reds.

There are various other somatic variations rather frequently seen in maize, but they are apparently not in-

herited. There are sometimes found variegated ears with a large patch of self-red cob but with little or no corresponding change in the color of the overlying grains. I have as yet no evidence that this somatic variation in cob color is inherited through the seeds of the self-red part of the cob. Such seeds apparently always produce ears with variegated grains and variegated cobs, just as do other seeds of the same parent ear. Of course variegated seeds from a self-red patch of cob occasionally give rise to a self-red ear, as discussed in detail in this paper, and such red ears always have self-red cobs, but this is also true of all self-red ears, whether or not they are produced by red or by variegated seeds and without respect to whether the part of the cob underlying these seeds is self-red, finely variegated, or entirely white.

Another form of somatic variation seen in ears of maize is the occurrence of patches of considerable size, the grains of which, though variegated, are much darker in color than the grains of the rest of the ear. Such patches of grains are often quite as strikingly distinct in appearance as patches of self-red grains, and are apparently even more likely to correspond exactly in outline with an underlying patch of self-red cob than are patches of self-red grains. Moreover, such dark, variegated grains often present a rather definite color pattern. The crowns are often made to appear almost solid red by the widening and convergence at the crown of narrow red stripes extending down toward the base of the grain particularly on the side opposite the germ. Another type of dark, variegated grains differs from the lighter, variegated grains of the same ear principally in the greater development of the somewhat washed-out red apparently underlying the dark red stripes of the variegation pattern proper. I have grown numerous progenies from dark and light variegated grains of the same ears, but as yet have no evidence that such somatic variations are inherited. Notwithstanding this, I have strains of maize breeding true to a very dark type of variegation, others to a medium

sort of variegation, and still others to exceedingly light types of variegation. There can be no doubt that some of these different types of variegation are inherited, but the mode of inheritance in crosses has not been fully worked out.

One other form of grain coloration that might be called an extremely dark type of variegation is to be noted. The grains are self-red throughout except for a nearly colorless crown formed by converging light stripes extending some way down the side of the grain opposite the germ, almost exactly the reverse of one of the types of dark variegation described above. Variegations of this sort behave in inheritance almost exactly like fully self-red grains, giving a large percentage of red-eared progeny. And these red ears are apparently always fully self-red, never showing the pattern of converging light lines seen in the parent seeds. Many such seeds have been included in the results recorded earlier in this paper where they were listed as "nearly self-red."

INTERPRETATION OF RESULTS

Any interpretation of the data presented here must take account of these facts: (1) that the more red there is in the pericarp the more frequently do red ears occur in the progeny, and (2) that such red ears behave just as if they were F_1 hybrids between red and variegated or red and white races. The development of red in the pericarp is evidently associated with and perhaps due to a modification of some Mendelian factor for pericarp color in the somatic cells. The zygotic formula of a plant homozygous for variegated pericarp may be designated as *VV*, and that of a plant heterozygous for variegated pericarp as *V*—. If in any somatic cell *VV*, from unknown causes, a *V* factor were transformed into a factor for self-color, *S*, that cell would then have the formula *VS*. Any pericarp cells descended from it would without further modification be red. If all the pericarp cells of a seed were thus descended, the seed would be self-red, just as it would

if the plant bearing it were a hybrid between pure red and variegated races. Moreover, one half of the gametes arising from such somatic cells would carry *V* and one half would carry *S*, just as if the plant were a hybrid of red and variegated types. Or, if both *V* factors were changed, the grains would be self-red as before, but all instead of half the gametes would carry *S*. If, however, the modification from *VV* to *VS* should occur very early in the life of the plant, or even of the embryo, all the ears of the plant might thereby become self-red, and one half of all the gametes both male and female might then carry *S* and the other half *V* as in the ordinary hybrid. Or the plant might then become a sectorial chimera with one variegated ear and one red ear, the gametes from the one side of the plant all carrying *V*. If the modification occur much later, say soon after the ear begins to form, there might then be merely a solid patch of red grains on an otherwise variegated ear. In this case only those gametes arising from these smaller masses of tissue would carry half *S* and half *V*. If, however, the modification occur after the grains begin to form, the latter might be perhaps three fourths red, or one half red, or merely have narrow stripes of red, depending upon the amount of pericarp directly descended from the modified cell. In this case it seems reasonable to assume that the larger the mass of modified tissue the greater the chance that the gametes concerned should carry *S*. Finally, if in certain grains the change never occurs, they should show no red and the gametes formed in connection with them should all carry *V*, none *S*.

Similarly, it may be assumed that in any cell of a heterozygous, variegated-eared plant, *V*—, the *V* factor may as before become an *S* factor. The effect on pericarp color would be exactly the same as in a homozygous, variegated plant, and, of the gametes arising from the modified tissue, one half would carry *S* as in the other case, but the other half, instead of carrying *V*, would carry no factor and would be represented by —.

If the interpretation suggested here is correct, it is to be expected that the more red there is in the pericarp of any seeds, *i. e.*, the larger the mass of tissue descended from the cell in which the change from *V* to *S* took place, the greater the chance that the female gametes concerned carried the factor *S*. With heterozygous, variegated-eared plants, *V*—, however, never more than half of the gametes concerned could carry *S* even in case of self-red grains, the other half of the gametes carrying no factor, —. Of the heterozygous, variegated ears the progenies of which have been reported here, some were selfed, some crossed with white, and some open-pollinated. From self-pollinated ears, self-red and nearly self-red seeds yielded 32 red-eared, 9 variegated-eared, and 14 non-red-eared plants, or practically 58 per cent. self-red. This excess of self-red ears may be due, in part at least, to the presence of the *S* factor in some of the male gametes concerned, but the numbers are too small to give very reliable indications. From similar ears that instead of being selfed were crossed with white, so that the results could not have been influenced by factors present in the male gametes, self-red and nearly self-red seeds produced 14 plants with red ears and 13 with non-red ears, or about 52 per cent. red. While these numbers are very small, the fact that no variegated ears were produced, but that every ear with any red color was self-red, is noteworthy. From the open-pollinated, heterozygous ears included in my cultures self-red seeds gave progenies consisting of 171 red-eared, 32 variegated-eared, and 102 non-red-eared plants, or about 56 per cent. red.

In case of homozygous, variegated-eared plants, *VV*, all the gametes associated with seeds that later become self-red could carry *S* only if both *V* factors of the somatic cells from which the gametes arise were changed to *S* factors. Because of the rarity of changes from *V* to *S*, unless both *V* factors are influenced alike by whatever causes the change, so that both change simultaneously to *S* factors, the chance is slight that more than one will ever change.

In the latter case only about 50 per cent. of the gametes associated with self-red grains of homozygous, variegated ears could be expected to carry *S*, just as in the case of heterozygous ears. None of the open-pollinated ears whose progenies I have grown were homozygous for variegated pericarp, and none of the homozygous ears that had been crossed with white contained any self red or nearly self-red seeds. The only data, therefore, that bear upon the point at issue are those obtained from self-pollinated, homozygous, variegated ears. The self-red and nearly self-red seeds of such ears produced 64 red-eared and only 25 variegated-eared plants, or about 72 per cent. self-red. This may mean that in some cases both *V* factors were changed to *S* factors, but the results may just as likely be due to the presence of *S* in an unusually large percentage of the male gametes concerned. The production of the 25 variegated-eared plants, however, is very good evidence that, in at least a very considerable number of cases, not more than one of the two *V* factors could have been changed to *S*.

If the change from *V* to *S* should happen to occur at such a time that the grain rudiments became sectorial chimeras consisting of say one half modified cells and one half unmodified ones, one half of the pericarp would be expected to show red color and the other half no color. It would be expected further that the chances of a particular gamete's arising from a modified or from an unmodified cell would be equal. If then one half of the gametes associated with these one-half-red grains arise from cells in which only one of the *V* factors has been changed to *S*, one fourth of the gametes should carry *S* and three fourths should carry *V*, or one fourth *S*, one fourth *V*, and one half —, depending upon whether the ears concerned are homozygous or heterozygous for variegated pericarp. Such grains from homozygous ears should, therefore, whether selfed or crossed by white, yield about one red ear to three variegated ones. Similarly, from heterozygous ears, grains with one half their pericarp red should

yield about one red to two variegated to one white if self-pollinated and one red to one variegated to two white if crossed by white. (This is on the assumption that no *S* factors are carried by the male gametes.) Let us assume that by lumping together all the seeds listed in the foregoing records as "more than one half red" and as "less than one half red" the whole lot would average about one half red, and compare the results with the expectation as noted above. From grains of these two classes from homozygous ears both selfed and crossed by white, there resulted 19 red-eared and 82 variegated-eared plants, or a ratio of about 1:4.3 instead of 1:3. From heterozygous ears self-pollinated grains of these two classes yielded 54 red-eared, 85 variegated-eared, and 52 white-eared plants, and similar grains crossed by white yielded 7 red-eared, 7 variegated-eared, and 20 white-eared plants, or ratios of 1.04:1.63:1 and 1:1:2.86 instead of 1:2:1 and 1:1:2, respectively. The observed ratios are certainly suggestive but must not be given undue importance, for there is no assurance that the seeds used really averaged one half red and no assurance that some of the male gametes in the case of the selfed seeds did not carry *S*.

We must now examine the results secured in generations later than F_1, and note whether the hypothesis under consideration applies equally well to them.

It will be recalled that F_1 red-eared plants that arose from homozygous, variegated ears which had been self-pollinated (see page 99) yielded in F_2 only red-eared and variegated-eared progeny. On our assumption the formula of the parent variegated ears was *VV*, but the red grains of these ears were *VS* and the gametes associated with them therefore either *V* or *S* or all *S*. Female gametes carrying *S* would have produced red ears in F_1 whether the male gametes carried *S* or *V*, and female gametes with *V* could not have produced red ears except when the male gametes uniting with them carried *S*. The F_1 red-eared plants must therefore have been *VS* or *SS*, the former being expected much more frequently than the

latter, owing to the rarity of *S* in male gametes. Only 7 such red ears were tested and all yielded red and variegated ears in typical Mendelian ratios, showing that all of them were *VS* like any F_1 hybrid between red and variegated races. Of two F_2 reds from selfed F_1's, one again yielded reds and variegates and one apparently bred true red. Three F_2 reds, from F_1 reds crossed by whites, yielded reds and whites only—typical Mendelian results throughout.

When F_1 red-eared plants arose from either homozygous or heterozygous, variegated ears that had been cross-pollinated by whites they yielded only red-eared and white-eared, never variegated-eared, offspring (see page 100), just as if they were F_1 ears of a cross of reds with whites. By hypothesis the parent variegated-eared plants were *V*— and *VV*, and their red grains *S*— and *SV* (or possibly *SS*). The gametes associated with such grains were therefore *S* and —, and *S* and *V* (or possibly all *S*). The male gametes from white races were all —. The F_1 plants were therefore *S*—, *V*—, and ——, only those with *S*— having red ears. The five red-eared F_1 plants that were tested produced in F_2 red-eared and white-eared plants in Mendelian ratios. Of the F_2 red-eared plants one bred true in F_3 and three again segregated into reds and whites.

When heterozygous, variegated, parent ears were self-pollinated, the F_1 red-eared plants behaved in some cases like hybrids of red with variegated races and in other cases like hybrids of red with white races (see page 99). Our assumption is that the variegated-eared parent plants were *V*— and their red grains *S*—. The gametes associated with these red grains were of course *S* and —. The male gametes of the same plants were doubtless largely *V* and —, though a few were probably *S*. The F_1 plants must therefore have been ——, *V*—, *S*—, *SV* or *SS*. Reds with *SS* would be expected only rarely, and of the 11 F_1 reds tested none had that formula, else they would have bred true in F_2. Seven of the 11 F_1 reds evidently were

S—, for they yielded F_2 progenies consisting of reds and whites only. Four of the 11 were obviously *SV*, for they yielded F_2's of reds and variegates only. Of the latter F_2 reds, one bred true in F_3 and four again segregated into reds and variegates.

From a self-red seed of a homozygous, variegated ear that had been cross-pollinated by a pure red race, an F_1 red-eared plant was produced and this plant bred true red in F_2. From a nearly self-red seed of the same variegated, parent ear, an F_1 red was produced but yielded reds and variegates in F_2 just as did a similar F_1 ear from a seed with narrow red stripes (see page 100). The variegated parent ear was *VV* and the red and near-red grains probably *VS*. The gametes associated with these grains were *V* and *S*. The male gametes were all *S*. Therefore the F_2 reds were in part *VS* and in part *SS*.

By way of summary, it is recalled that, in all, 28 F_1 red-eared plants were tested by F_2 progenies. Only one of these bred true and that one came from a red grain of an ear that had been cross-pollinated by a pure red race. Disregarding the three F_2 red-eared plants thus produced and the 9 red ears produced from seeds of variegated ears that had been cross-pollinated by white races and that therefore could not have bred true, there remain 16 F_1 reds, none of which bred true in F_2. Had these F_1 red-eared plants behaved as did the F_1 green-leaved plants produced by green branches of variegated-leaved parents in Correns's experiments, approximately 5 of the 16 should have bred true. It will be recalled that Correns found that such green branches always produced green-leaved and variegated-leaved plants in the ratio of 3:1, and that one of the three bred true and the other two again segregated, just as must have happened if the green branch had been a part of an F_1 hybrid of green with variegated instead of a part of a homozygous variegated plant.

The difference between *Zea* and *Mirabilis* is, however, not a fundamental one, but is due merely to the circum-

stance that *Mirabilis* has perfect flowers while *Zea* is monecious. In *Mirabilis* both male and female gametes of a green branch arise from somatic cells in which the *V* factor has changed to a *G* factor. If a change in only one *V* factor is responsible for the production of the green branch, the somatic cells of such a branch must all be *VG* and the results reported by Correns are the only ones to be expected. With *Zea mays,* however, all the grains of one ear of a variegated-eared plant might arise from cells having *VS,* so that half of the female gametes would carry *S,* while little or no corresponding change might take place in the staminate inflorescence and therefore no (or very few) male gametes would carry *S*. From such an ear of maize only about one half, instead of three fourths, of the F_1 plants should have red ears and none (or very few), instead of one third, of the F_1 plants should breed true.

The occasional green plants (*"a"* per cent.) arising from variegated branches in Correns's experiments with *Mirabilis* are more nearly comparable to F_1 red-eared maize plants than are the green plants arising from green branches. It is quite conceivable that on a variegated branch the male gametes might arise from cells that are *VG,* while the female gametes arise from cells that are *VV,* or the reverse, though this difference between male and female gametes would hardly be so common an occurrence as with maize where the staminate and pistillate inflorescences are situated so far apart. It is worthy of note in this connection that of the occasional green plants produced by selfed seed of variegated plants in Correns's experiments with *Mirabilis* (see diagram, Fig. 2), less than one third bred true and more than two thirds segregated into green and variegated. (Correns indicates this merely by the signs $<$ and $>$ in connection with 33 per cent. and 66 per cent. respectively, in his diagram, and gives no indication of how much less than 33 per cent. bred true or how much more than 66 per cent. segregated.)

De Vries's results with *Antirrhinum* yield readily to

the same analysis used with *Zea* and *Mirabilis*. Selfed seed from striped-flowered branches gave a small per cent.—from 2 to 10—of red-flowered plants. Only a few of the red-flowered plants were tested and these were found to yield 76 per cent. red to 24 per cent. striped. Selfed seed from red-flowered branches of striped-flowered plants yielded 71 per cent. red-flowered and 29 per cent. striped-flowered plants, approximating the 75 per cent. and 25 per cent. indicated by Correns's results with *Mirabilis*. None of these red-flowered plants bred true, but only one test, and that of only a few plants, was made. The results were 84 per cent. red-flowered and 16 per cent. striped-flowered plants. It seems quite likely that had de Vries tested more red-flowered plants he would have found some of them to breed true.

Correns's results with striped and red flowers of *Mirabilis* differed in one important respect from his results with variegated and green plants of the same species, as well as from the principal results with *Zea* reported here and from de Vries's results with striped-flowered and red-flowered forms of *Antirrhinum*. When red-flowered plants arose from striped-flowered varieties of *Mirabilis*, they behaved just as did the green plants that arose from variegated forms. But selfed seeds from wholly red-flowered branches of otherwise striped-flowered plants yielded little if any larger percentages of red-flowered plants than did selfed seeds from striped-flowered branches of the same plants. It would seem that in case of *Mirabilis* flowers, when the self pattern arises as a somatic variation from the variegated pattern there is no corresponding change in the Mendelian factors for these patterns. In case of seed-sports from variegated-flowered to red-flowered plants, however, the factors for variegation are affected just as in case of green plants arising from variegated ones and of red-eared maize plants arising from variegated-eared ones. The apparently non-inherited somatic variations of maize plants, noted briefly earlier in this paper, are possibly of the same nature as

the somatic variations in variegated flowers of *Mirabilis*. Some of these variations in maize are self-red cob patches on otherwise variegated cobs, and dark, variegated grains occurring in patches or scattered over light, variegated ears.

General Considerations

The experiments of de Vries, Correns, Hartley, and East and Hayes, as well as the records reported in this paper, all indicate that certain somatic variations are inherited in strictly Mendelian fashion. All these somatic variations consist in the appearance of self-colors on plants that are normally variegated in pattern. The fact that variegated plants occasionally throw both bud-sports and seed-sports with self-colors is not, in general, to be taken as an indication that the variegated plants in question are heterozygous. Such behavior seems to be inseparably associated with variegation. Correns has pointed out (*loc. cit.*) that variegated *Mirabilis* plants can not be considered mosaics of green and "chlorina" types due to heterozygosis, since they do not segregate into chlorina and green, but into variegated and green. The same reasoning applies to variegation in the color of maize ears. Variegated-eared plants do not throw reds and whites, but reds and variegates. The conclusion seems irresistible that self-color occurring as a somatic variation is due to the change of a Mendelian factor for variegation into a factor for self-color. If this be granted, the behavior of these variations in later generations is a mere matter of simple Mendelian inheritance.

From the title of his paper and the tone of his discussion, it is clear that Correns regards, as the most significant feature of these inherited somatic variations, the change from a homozygous to a heterozygous condition. He even refers to them as cases of "vegetativen Bastardierung" or "autohybridization." To me, however, the essential feature is the change of one Mendelian factor into another. The fact that this modification of genetic factors results in a change from homozygosis to heterozy-

gosis seems wholly incidental. It follows from the circumstance that usually only one of the two *V* factors of somatic cells is modified. My own data do not in fact show that the change always affects only one of the factors at a time. While the results prove that this is true in a part of the cases at least, the F_1 ratios suggest the possibility of both factors being modified in some cases.

It is of course utterly impossible at the present time to conceive of the cause or even of the nature of this change in factors from *V* to *S*. We can only conjecture at present as to whether the change may possibly be associated with changing metabolic processes in the maturing plant, or perhaps be connected in some way with changing external influences, or even be a quality inherent in the *V* factor itself. It is perhaps significant that in maize, at least, the change, whatever its cause, occurs very rarely early in the life of the plant and apparently becomes increasingly more frequent as the plant matures. Wholly red ears in variegated-eared plants are extremely rare; large patches of red grains are somewhat less rare; individual red grains occur on most variegated ears; red stripes on the individual grains are very frequent, in fact all but universal in some strains, though in other strains —very light variegated ones—there may be only a few striped grains on a whole ear, the others being wholly colorless. As a matter of fact, even the presence of an ear with red pericarp throughout on a variegated-eared plant may not be good evidence that the change in factors occurred before the ear began to form. If the change took place before the ear was laid down, it would seem that the cob should always be self-red, since the red-eared progeny of such modified grains of the variegated parent plant invariably have red cobs, and cob and pericarp colors are coupled absolutely in later generations. But red ears, or nearly red ears, with light variegated instead of red cobs, have been found to occur as somatic variations on variegated-eared plants. Such behavior suggests that sometimes the factor change may occur almost simul-

taneously in the rudiments of every grain so that the grains become self-red while the cob remains variegated. We might, of course, account for the appearance of self-colored grains on a variegated cob on the basis of separate factors for cob and pericarp color[10] by the assumption that one of these factors may be modified while the other remains unchanged. But we should then have the no less difficult problem of accounting for the universal appearance of red cobs with F_1 red ears without respect to whether the parent grains stood on red or variegated cobs.[11]

Forced to its logical limit, our conception of the *V* factor is that of a sort of temporary inhibitor, an inhibitor that sooner or later loses its power to inhibit color development, a power that once lost is ordinarily never regained. Of course it may be that there is present in variegated maize merely a dominant factor for self-color, *S*, that is temporarily inactive, but that sooner or later becomes permanently active. Even if this be true, *S* as an active factor and *S* as an inactive factor are certainly as distinct in inheritance as they are in development and therefore deserve to be designated separately. And since in one case there results self-color and in the other variegation, the factors may as well be called *S* and *V* as anything else. It is of course also conceivable that the *S* factor may repeatedly arise *de novo,* though this seems very unlikely.

Whatever our conception of the nature of the factors for variegation and for self-color in maize ears, these factors are certainly as distinct in inheritance as any two factors could well be. Moreover, there is abundant evidence, which can not be given here, that they are strictly allelomorphic, as indeed they must necessarily be if one arises by modification of the other—this on the assumption that the factors are definitely localized in certain

[10] Evidence that there are distinct factors for cob and pericarp color was presented in a previous paper on coupling and allelomorphism in maize. Ann. Rpt. Nebr. Agr. Expt. Sta., 24: 59–90. 1911.

[11] This problem is discussed in another paper on the simultaneous modification of distinct Mendelian factors. AMER. NAT., 47: 633–636. 1913.

chromosomes. Furthermore, these factors are to be regarded as *pattern* factors. Though they must influence the development of the pigment in order to produce a pattern at all, they are now known to be distinct in inheritance from the factors for pigment—a fact that I have been able to show by use of a race of maize with a peculiar brown pericarp in addition to races with red pericarp.

SUMMARY

A somatic variation in maize is shown to be inherited in simple Mendelian fashion. The variation has to do with the development of a dark red pigment (or in one stock a brown pigment) in the pericarp of the grains, often associated with the development of an apparently similar pigment in the cob and husks.

Plants in which this pigment has a variegated pattern may show any amount of red pericarp, including wholly self-red ears, large or small patches of self-red grains, scattered self-red grains, grains with a single stripe of red covering from perhaps nine tenths to one tenth of the surface, grains with several prominent stripes and those with a single minute streak, ears with most of the grains prominently striped and ears that are non-colored except for a single partly colored grain, and probably also plants with wholly self-red and others with wholly colorless ears.

It is shown that the amount of pigment developed in the pericarp of variegated seeds bears a definite relation to the development of color in the progeny of such seeds. This relation is not such that seeds showing say nine tenths, one half, or one tenth red will produce or even tend to produce plants whose ears as a whole or whose individual grains are, respectively, nine tenths, one half, or one tenth red. Experimental results indicate rather that the more color in the pericarp of the seeds planted the more likely are they to produce plants with wholly self-red ears, and, correspondingly, the less likely to yield plants with variegated ears.

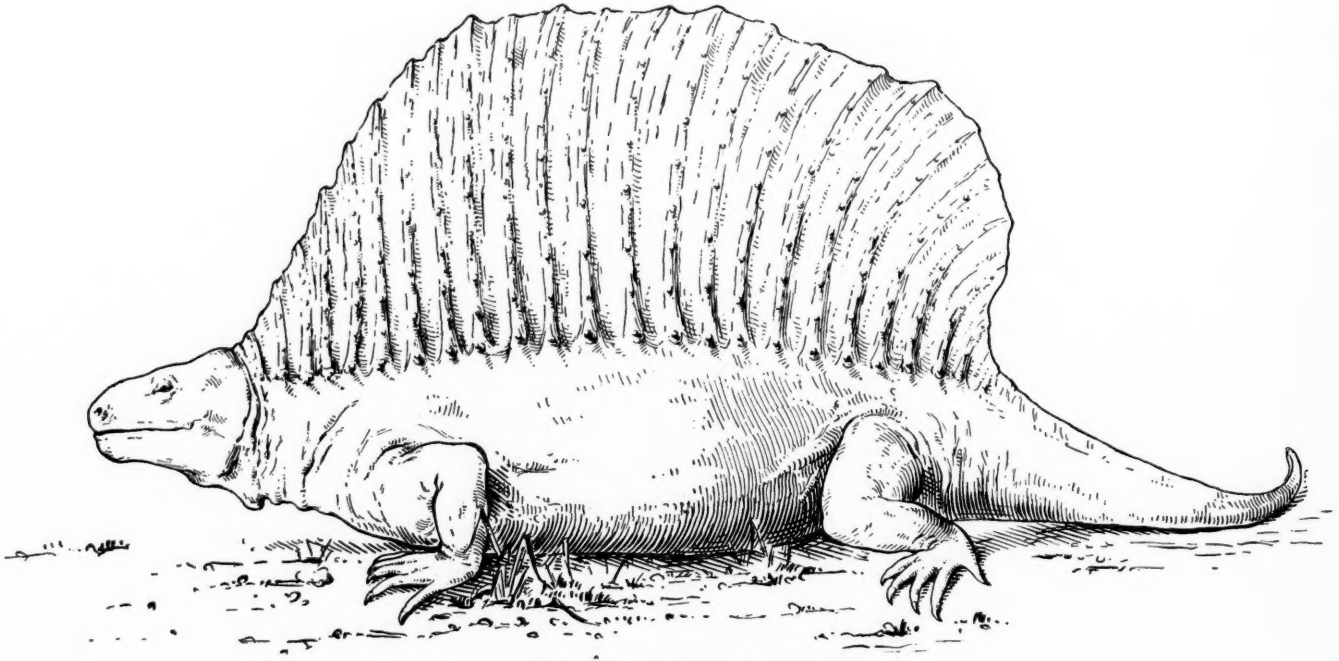
Self-red ears thus produced are shown to behave in in-

heritance just as if they were hybrids between self-red and variegated races or between self-red and non-red races, the behavior in any given case depending upon whether the parent variegated ears were homozygous or heterozygous for variegated pericarp and whether they were self-pollinated or crossed with white.

It is suggested that these results may be interpreted by the assumption that a genetic factor for variegation, *V*, is changed to a self-color factor, *S*, in a somatic cell. All pericarp cells directly descended from this modified cell will, it is assumed, develop color, and of the gametes arising from such modified cells one half will carry the *S* factor and one half the *V* factor if only one of the two *V* factors of the somatic cells is changed, or all such gametes will carry *S* if both *V* factors are changed.

The *V* factor is thought of as a sort of temporary, recessive inhibitor that sooner or later permanently loses its power to inhibit color development, becoming thereby an *S* factor. Or it may be that the dominant factor, *S*, is temporarily inactive, but sooner or later becomes permanently active. Again, the *S* factor may repeatedly arise *de novo*. The cause of any such change in factors is beyond intelligent discussion at present.

The results of Correns with *Mirabilis* and of de Vries with *Antirrhinum* are shown to be subject to the same analysis as that used to interpret the results secured with maize.



RESTORATION OF *Edaphosaurus cruciger* COPE.

RESTORATION OF EDAPHOSAURUS CRUCIGER COPE

PROFESSOR E. C. CASE
UNIVERSITY OF MICHIGAN

IN the year 1882 Cope described from the Permian beds of Texas, an imperfect reptilian skull which he called *Edaphosaurus pogonias*. Two years later he described for the first time, the wonderful vertebræ with elongate spines bearing lateral projections on the sides. These vertebræ he assigned to the same genus as the skull but later they were removed to a separate genus as he considered that the two specimens represented different forms of reptilian life. The vertebræ with long spines and cross pieces were placed in the genus *Naosaurus*—"Ship-lizard," a name suggested by the fancied resemblance of the spines with their lateral projections to the masts and yard-arms of a full-rigged ship.

From the time of the original description until 1907 the two genera were regarded as distinct but in that year Case[1] suggested that the two genera should be united and that the skull described as *Edaphosaurus* by Cope belonged with the vertebral column and limb bones described under the name *Naosaurus*. The similar condition of elongate spines, but without cross pieces, on the vertebræ of the carnivorous genus *Dimetrodon* very naturally led to the belief that the two forms *Edaphosaurus* and *Dimetrodon* were similar in other parts of the body and *Naosaurus* merely exhibited something of the extravagance in spines, rugosities, tubercles, etc., which is such a common feature in the most highly specialized members of any group which is approaching the final stages of its family or generic life. The close relationship of the two genera was so probable that it was accepted by all paleon-

[1] Publication 55, Carnegie Institution of Washington.

tologists and even Case was very reticent in his suggestion that they were much farther apart than was usually thought. Following the generally conceived idea of *Naosaurus* a composite mount was prepared in the American Museum of Natural History in New York in which the skull and limb bones of a *Dimetrodon* were associated with the vertebral column of a *Naosaurus*. This restoration was published by Dr. Osborn in the Bulletin of the American Museum and a model of the creature in the flesh was prepared under his direction by Mr. Chas. Knight. Case in his "Revision of the Pelycosauria of North America" republished this restoration by Osborn but at the same time published an alternative restoration in which the skull described as *Edaphosaurus* was associated with the vertebral column of *Naosaurus* and the two genera were united under the former name, as it had priority.

The composite restoration prepared at the American Museum has gained wide circulation in the text books but later discoveries have shown that it was unfortunate. In the summer of 1911 Dr. F. v. Huene, of Tübingen, while a guest of the joint expedition from the universities of Chicago and Michigan to the Permo-Carboniferous beds of New Mexico, discovered the remains of a skeleton of *Edaphosaurus* in which both the skull and a portion of the vertebral column were preserved. As the vertebræ bore the typical cross-pieces of the genus *Naosaurus* the identity of the two genera was established but new evidence was speedily coming; Case in the summer of 1912 discovered in the Permo-Carboniferous beds of Archer County, Texas, the nearly perfect vertebral column of an *Edaphosaurus* (*Naosaurus*) *cruciger* Cope with the limb bones, and a crushed skull, identical with the skull originally described as *Edaphosaurus*.

From this skeleton, now preserved in the museum of the University of Michigan, the author has prepared the restoration shown in Fig. 1. The only conjectural parts are the size of the feet and the length of the tail; the re-

mainder is based upon careful measurements from a single specimen. So far from being a carnivorous, raptorial animal similar to *Dimetrodon, Edaphosaurus* was harmless, molluscivorous or insectivorous with possibly some ability to masticate vegetable matter. The edges of the jaws were lined with sharp conical teeth and upon the palate and the dentary bones were strong plates supporting numerous blunt, conical teeth. The head in all specimens recovered seems rather small for the size of the body and in this is peculiar in the Permo-Carboniferous reptilian fauna, in which the reverse is the rule. The shape of the head in the restoration is taken from the nearly perfect and undistorted skull in the museum of the University of Chicago. The elevated dorsal spines begin with the third vertebræ and speedily reach a considerable height. The lateral projections are elongate at the base of the spine but above the middle are reduced to mere nodules irregularly arranged. The author is not in accord with the suggestion made by Jaekel and Abel that the spines were separate, and can see no reason for the suggestion made by the former that the spines were movable. The strongly interlocking zygapophyses render such an idea impossible to any one familiar with the skeleton. Nor does the author believe that the spines were of any use to the creature as offensive or defensive weapons; rather, as he has frequently expressed himself, he believes that they were in the nature of excessive growths which may have had their inception and impetus in some useful function, but grew beyond that use as the animal became more specialized. The union of the spines into a thin dorsal fin is far more probable and the idea is supported by the presence of rugosities and the channels of small nutrient vessels such as would lie beneath a thick dermal covering. The anterior and posterior faces of the bases of the spines have sharp, low ridges which give place to shallow grooves farther up the spine; only near the top are the spines similar on all sides. Moreover in the living genus *Basiliscus,* which has elevated dorsal spines,

and in the genera of the chameleons in which the same thing occurs, for example, *Chameleo cristatus* Stutch., the spines are united into a thin dorsal crest by the integument and are further united by a thin membrane carrying scattered muscle fibers. The outline of the dorsal fin shown in the restoration is suggested by all the specimens in which the spines have been preserved. The sharp recurvature of the spines in the lumbar region is less pronounced in the specimen from which the restoration was drawn than in some other and it is possible that in other species there was even more of an overhang of the posterior end. The spines are abruptly shortened in the pelvic region and rapidly decrease on the tail. The length of the tail is not known but in all probability was elongate rather than short and stumpy.

The limbs were short and heavy with the forearm and foreleg shorter than the proximal segment of the limb, a condition which is quite common in slow moving forms or those of aquatic or palustrial habit, and just the reverse of the condition found in the active, raptorial *Dimetrodon*. The bones of the feet have not been found in position, but in the great Brier Creek Bone-bed in Archer County, Texas, excavated by an expedition from the University of Michigan in the summer of 1913, numerous large foot bones of a character different from those of *Dimetrodon* or the cotylosaur *Diadectes* were found associated with the spines of *Edaphosaurus* and with large claws. It is believed that the foot of that animal was of goodly size and armed with sharp claws well fitted for digging in the soft earth or vegetation, tearing open rotten logs and overturning rocks in search of food.

It has been noted by all collectors in the Texas beds that isolated vertebræ of *Edaphosaurus* are among the most common fossils found but that any portion of an associated skeleton is extremely rare. This has led to the suggestion that the remains of the animals were transported for some distance after death, probably by rivers from a higher land.

Edaphosaurus was a highly specialized creature, sluggish in movement and entirely harmless, living upon molluscs, insects and perhaps vegetation. It probably lived in the woods or near swamps at some distance from the lowlands upon which were deposited the deltas which make up the Wichita and Clear Fork formations.

In conclusion the author wishes to express his thanks to Dr. Ruthven, of the University of Michigan, for many valuable suggestions in arranging the pose and proportions of the restoration, and to Mr. Irwin Christman, of the American Museum, for the painstaking care with which his suggestions have been followed in making the drawing.[2]

[2] A full account of the known specimens of *Edaphosaurus* and *Naosaurus* and a complete synonymy of the two genera will be found in Publications 55 and 181 of the Carnegie Institution of Washington.

SHORTER ARTICLES AND DISCUSSION

HUMIDITY—A NEGLECTED FACTOR IN ENVIRONMENTAL WORK

AN admittedly rough but probably fair estimate of the relative interest which has been taken in the relation of the various environmental factors to insects, at least, may be made from the fact that Bachmetjew in his admirable compilation[1] of the work along these lines devotes, in round numbers, four hundred pages to temperature, one hudred and fifty to food and chemicals, seventy to light, forty-five to humidity, fifteen to electricity and magnetism and thirty to mechanical and other factors. Why is it that temperature is given about a third more attention than all the other factors put together? Is it true that it is nearly ten times as interesting or important as humidity?

A partial answer to the first question undoubtedly is that temperature is easily controlled as well as measured, whereas humidity, for example, is not easily controlled and the means of measuring humidity in small containers are untrustworthy and expensive. Furthermore, work with temperature gives results. The unfortunate part is that these results have usually been ascribed wholly to temperature.

In the course of some work at the Carnegie Station for Experimental Evolution I found that I could change to a surprising extent the markings on the larvæ of a moth (*Isia isabella*) by varying the temperature at which they fed and moulted. However, such changes were much more definite when the temperature was kept constant and humidity varied. I did not have the necessary apparatus for getting accurate control of either factor, but I feel confident that temperature had little or no direct influence. It was acting through its influence upon humidity.

It would seem unnecessary to urge upon experimenters such a fundamental principle in the logic of cause and effect, but the fact is that with only two or three exceptions none of the more than a hundred papers having to do with the effect of temperature upon insects tell us anything about the effect of temperature

[1] "Experimentelle Entomologische Studien vom physikalisch-chemischen Standpunkt aus." Zweiter Band. Sophia, 1907.

per se. A few state that the atmosphere was "moist" or "dry," but even then how moist or how dry is not usually mentioned unless it is believed to be saturated or absolutely free from moisture. It is clearly incumbent upon the one who makes such a criticism to show, either by his own work or in a review of that of others, that humidity is a factor of such importance that the criticism is worth the making—especially since the point is so self-evident and has been made in the past. The following notes are an attempt to justify the preceding.

The experiments of many workers show that when lepidopterous pupæ are subjected to abnormal temperature part, at least, of the adults which emerge differ from the normal. The observations have usually been made on color changes, and Fisher[2] especially has shown that warm conditions (36° to 41° C.) produce the same or similar effects as do cold conditions (0° to 10° C.), also that hot conditions (42° to 46° C.) produce effects which are similar to those produced by freezing (—20° to 0° C.). Fisher apparently had no means of successfully controlling the humidity but Tower[3] claims to have had this in his "Investigation of Evolution in Chrysomelid Beetles of the Genus *Leptinotarsa*" and he obtained similar results, stating them as follows:

> The result produced by either a higher or a lower temperature is the development of a greater amount of pigmentation and a consequent melanic tendency in variations. This stimulus in both directions to increased pigmentation reaches a maximum between 5° and 7° C. deviation from normal. Beyond these, as the temperature further deviates, there is a rapid fall in melanism, first to the normal, and then to a condition below normal, until a marked albinic tendency is found; and this decrease in pigmentation continues until the zero point is reached, beyond which no pigment whatever is produced. The zero point is reached much sooner, however, in high-temperature experiments than in low.

Tower then gives the results of experiments in which all the environmental conditions, except humidity, are "normal." Normal humidity for *Leptinotarsa decemlineata* is taken as ranging from 43 per cent. to saturation with an average of 74 per cent. The humidity in various experiments ranges from 10 per cent. to saturation. The lowest natural humidity of which I have seen a record is 5 per cent. It occurred in Death Valley, California,

[2] See *Archiv für Rassen- und Gesellschafts-Biologie*, 1907, IV, pp. 761–793, for Fisher's statement concerning criticisms of his conclusions.

[3] Carnegie Institution of Washington, Publication No. 48, 1906.

where the monthly means for May to September inclusive varied from 20 per cent. to 27 per cent. The annual mean at Cairo, Egypt, is 56 per cent. and at Ghardaia (Algerian Sahara) is 50 per cent. at 7 A.M. and 26 per cent. at 1 P.M. The humidity at Buitenzorg, Java, during the height of the rainy season fluctuates between 70 per cent. and 97 per cent. during the day. Naturally, when dew is being deposited the humidity is practically 100 per cent. It will be seen then that even Tower's extreme averages (see below) are not beyond the range of possibility in nature, although they are as great as it is possible to use in experimental work, since at an average of 34 per cent. humidity only 0.4 per cent. of the larvæ reached the adult stage and atmosphere can not be kept supersaturated.

The beetles were seriated according to an arbitrary scale in which "20 equals total melanism and 0 total albinism." It is difficult to suggest a better method of measuring the extent of melanism than this, although we could wish for diagrams to aid us in grasping just what the scale means. I have tabulated the experiments and interpolated the normal data.

Relative Humidity		Per Cent. of Mortality	Melanism	
Average	Range		Mode	Range
100	100–100	90	4	2–9
95	82–100	30	7	3–11
84	55–100	15	12	7–16
74	*43–100*	*?*	*9*	*5–13*
66	33–100	35	11	6–18
60	30–100	80	5	3–11
50	25–83	92	3	1–7
34	10–55	99.6	2	1–4

It will be seen that mortality increases rapidly as the humidity departs from normal but this can not account for the change in color since the range of melanism is doubled and in three of the experiments even the mode falls below the normal range. As stated by the author:

> The results of experiments with deviations of humidity are almost exactly the same as those which were obtained from experiments with deviations of temperature. Such deviations from the normal either toward an increase or a decrease, produce up to a maximum increased pigmentation and a consequent melanic tendency, but beyond this the effect is reversed, pigmentation is retarded, and the tendency toward albinism becomes more and more pronounced as the deviation from the normal becomes greater.

The point which concerns the present discussion is that not only does humidity have a definite regularly acting influence, but that its results are similar to those of temperature and, as with temperature, plus and minus variations of certain intensities bring about similar effects. If, as has usually happened, the humidity is not controlled in experimental work on the effect of temperature, how can it be said that the observed results are the effect of changes in temperature?

Tower made certain experiments in which both temperature and humidity are abnormal, normal average temperature being taken as 22.2° C. Unfortunately, proof reading or something of the sort was faulty when it came to publication. Experiment 26 would be the most valuable for our present purpose, but the table includes records of relative humidity 35 and 39 per cent. above normal, *i. e.*, relative humidities of 109 and 113 per cent., respectively, if, as in the other experiments, 74 per cent. is "normal" humidity. These are clearly impossible. The text figure illustrating this experiment does not help us since humidities are not given and furthermore the temperatures in the figure are rather consistently one degree different from those given in the table. Since there are two errors in text-figure 15, which illustrates the experiments with humidity as the only variable, it is likely that the figure is the thing that is at fault here. Several other similar discrepancies could be pointed out (as, for example, the temperatures in experiment 24, which concerns the combination effect of humidity and temperature) but it is probable that the author's notebook records are correct and the temperature discrepancies in the published report are so slight that we may accept his conclusion. It is

> that when temperature and moisture are the variables in a given environmental complex, the trend of general color modification is controlled by moisture (relative humidity), excepting in conditions where the temperature deviation is so excessive that the ordinary physiological and developmental processes are greatly inhibited. In experiments approximating natural environmental complexes, however, moisture is the dominant factor in influencing coloration.

Even if there were no other reasons for urging the necessity of taking humidity into account, I feel that Tower's work would be ample justification. Before taking up those reasons let us notice several cases where, on account of the striking results of the experiments, we must regret our lack of information as to the real cause or the relation of the several causes.

This same work of Tower is one of them. The effects just noted were merely ontogenetic. However, he made other experiments in which the effect seemed to be passed on by heredity. The factors in the various experiments with *L. decemlineata* were 35°, 45 per cent. and low atmosphere pressure (p. 287); "hot, dry" (p. 288); "hot, dry and low pressure" (p. 288); and "hot, moist" (p. 291), probably 31.2°, 94 per cent. Those with *L. multitæniata* were 30° and saturation (p. 292 and p. 293); and the one with *L. undecemlineata* was "10 C. above the average and a relative humidity of 40 per cent." The work is of such importance because of its pioneer character that it would be ungracious to complain too strongly, but the fact is that it is impossible to tell from the data given whether the effects are caused by humidity or by temperature or by a combination of the two. Bateson's idea that there are no effects to be explained need not concern us here.

There is a long series of interesting papers starting in 1895 by Fischer. As has already been mentioned, he finds that certain high temperature grades produce effects which are similar to those produced by certain low temperature grades. The conditions of humidity are rarely mentioned, not to say considered. However, he occasionally confesses that they are important, as when he tells us[4] that it is necessary to have the warm air dry and the cold air moist in order to get similar forms of *Vanessa* by the application of moderate cold and moderate heat. I suspect humidity largely enters into the other experiments also for in one with high temperature,[5] which gave the same results as certain low temperatures and presumably high humidity he says the humidity was high.

Like Tower's experiments with beetles these concern color alone. Pictet[6] and Federley,[7] especially, have considered the effect of environmental factors upon the form of lepidopterous scales. Federley calls his work "Temperatur-experimente" and Pictet "Influence de l'Humidité" but neither enables us to differentiate the effects of the two factors, although both obtained striking results. Kominsky[8] modified to a considerable extent

[4] *Algemeine Zeitschrift für Entomologie,* VIII, p. 274, 1903.

[5] *Illustrierte Zeitschrift für Entomologie,* IV, p. 134, 1899.

[6] *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève,* XXXV, Fasc. 1, 1905.

[7] *Festschrift für Palmen,* No. 16, Helsingfors, 1905.

[8] *Zool. Jahrbücher. Abt. für Allg. Zool. und Physiologie,* pp. 321–338, 1911.

not only the color and form of scales but also the form of antennæ, legs and other body parts of Lepidoptera. He exposed the pupæ to 42.5° C., humidity not given; 38° to 39° C. and 42° to 43° C., relative humidity 80; 8° C., "high humidity"; 0° C., "very high humidity"; —7.5 to 5° C., relative humidity 80–90 and 50; and —11° C., humidity not given. For the most part the humidity was high and probably had much to do with the results, but we can not be certain.

All the experiments just considered were made upon pupæ. It should be remembered that only about one fourth of the weight of lepidopterous pupæ consists of solids, and that the only way they can replace fluids lost by evaporation is by chemical changes in these solids. It is probable that they do so to some extent, although this has not been accurately determined. It is known that under normal conditions pupæ lose in weight and the percentage of solids increases. Naturally, a change in the humidity of the surrounding air would modify this physiological process and it is difficult to believe that it has not quite as much effect as changes in temperature, the humidity remaining the same. It is easy to see that, if the air is made more absorptive or less absorptive either by the temperature changes themselves or by other means, and then the physiological activities are slowed or quickened by temperature changes, the effects will be much greater and might easily pass as due entirely to the temperature changes.

The species which have wet and dry season forms in regions where the temperature is fairly constant throughout the year, as well as the tendency for the animals of moist regions to be melanic and of arid regions to be light colored, speak for the important influence of humidity. But there is another point in distribution to be considered. The study of distribution was long, and still is, largely an effort to get the ranges of animals and plants to fit isotherms. When yearly averages do not work, winter minima or summer maxima or accumulated temperatures are tried. The success which often attends these efforts shows that man is very ingenious and also that temperature is really one of the controlling factors, but it does not show that it is the only factor or, in fact, that it has any direct influence.

The areas of grassland and forest in North America cut across isotherms as though they were merely political boundaries but Transeau[9] has shown that if we plot the ratio of temperature to

[9] AMER. NAT., XXXIX, pp. 875–889, 1905.

humidity we get a very close correspondence between distribution and climatic factors. Schimper[10] has brought together a great deal of evidence which indicates that, as far as plants are concerned, even the major divisions of the world's surface into arctic, temperate and tropical are fundamentally a question of the demand for and supply of water.

Furthermore, if recent climatic changes have an effect upon the origin of new characters and the distribution of the organisms possessing certain characters, humidity is deserving of more attention than temperature, since practically the only evidence we have of such changes concerns humidity.

It should not be forgotten that even aquatic organisms are subject to what amounts to changes in humidity. Peat bog plants take on many characteristics of a desert flora, although their roots are covered with water. It is water, however, which is not easily available, because of the chemicals which it carries. It is water which is physiologically dry.

Finally, the great amount of work which has been done upon artificial parthenogenesis and related subjects is, in a way, a study of the influence of environmental factors. The obvious factors concerned have usually been various chemicals but at foundation humidity, in a broad sense, the addition or withdrawal of water by osmosis seems to be a factor of prime importance.

FRANK E. LUTZ

AMERICAN MUSEUM OF NATURAL HISTORY

[10] "Plant Geography upon a Physiological Basis," translated by W. R. Fischer. Oxford, 1903.